No place to go and nowhere to be? Characterising demography of the southern scrub-robin (*Drymodes brunneopygia*) using molecular and modelling tools for conservation

Jolene Scoble

Submitted for the degree of Doctor of Philosophy August 2012
School of Earth and Environmental Sciences, The University of Adelaide & Commonwealth Scientific and Industrial Research Organisation (CSIRO)
Table of contents

Table of contents ......................................................................................................................... i
Thesis summary .............................................................................................................................. iv
Declaration of Authorship ............................................................................................................... vi
Thesis acknowledgements ............................................................................................................. vii
Chapter 1: ....................................................................................................................................... 9
General Introduction ....................................................................................................................... 9
  Human impacts: habitat change and loss .................................................................................... 9
  Human impacts: climate change ................................................................................................. 12
  Conservation in a brave new world ............................................................................................. 15
  A model species: the southern scrub-robin .............................................................................. 17
  Project Objectives ..................................................................................................................... 20
Chapter 2: ....................................................................................................................................... 21
  A case for incorporating phylogeography and landscape genetics into species distribution
  modelling approaches to improve climate adaptation and conservation planning ................. 21
    STATEMENT OF AUTHORSHIP ......................................................................................... 22
    Permission to reprint .............................................................................................................. 23
Chapter 3: ....................................................................................................................................... 38
  Isolation via 454 sequencing, and characterisation of microsatellites for Drymodes brunneopygia,
  southern scrub-robin (Aves: Petroicidae): a species at risk due to substantial habitat loss and
  climate change ............................................................................................................................ 38
    STATEMENT OF AUTHORSHIP ......................................................................................... 39
    Permission to reprint .............................................................................................................. 40
Chapter 4: ....................................................................................................................................... 45
  Between a rock and a hard place – molecular implications of habitat fragmentation and
  protection for the Australian southern scrub-robin (Drymodes brunneopygia) ....................... 45
    STATEMENT OF AUTHORSHIP ......................................................................................... 46
  Abstract ....................................................................................................................................... 48
  Introduction ................................................................................................................................. 49
  Materials and methods ................................................................................................................ 51
  Results ........................................................................................................................................ 57
  Discussion ................................................................................................................................... 68
  Conclusion ................................................................................................................................. 72
  Acknowledgements ................................................................................................................... 73
  Supplementary section ................................................................................................................ 74
Chapter 5: ....................................................................................................................................... 75
<table>
<thead>
<tr>
<th>Chapter</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>Home sweet home: habitat structure and invasive species drivepatterns of local genetic diversity in the southern scrub-robin (<em>Drymodes brunneopygia</em>)</td>
<td>104</td>
</tr>
<tr>
<td></td>
<td>STATEMENT OF AUTHORSHIP</td>
<td>105</td>
</tr>
<tr>
<td></td>
<td>Abstract</td>
<td>107</td>
</tr>
<tr>
<td></td>
<td>Introduction</td>
<td>108</td>
</tr>
<tr>
<td></td>
<td>Materials and methods</td>
<td>110</td>
</tr>
<tr>
<td></td>
<td>Results</td>
<td>117</td>
</tr>
<tr>
<td></td>
<td>Discussion</td>
<td>126</td>
</tr>
<tr>
<td></td>
<td>Conclusion</td>
<td>131</td>
</tr>
<tr>
<td></td>
<td>Acknowledgements</td>
<td>131</td>
</tr>
<tr>
<td></td>
<td>Supplementary section</td>
<td>132</td>
</tr>
<tr>
<td>7</td>
<td>Mapping the future: understanding how the environment shapes the distribution and genetic diversity of the southern scrub-robin (<em>Drymodes brunneopygia</em>)</td>
<td>135</td>
</tr>
<tr>
<td></td>
<td>STATEMENT OF AUTHORSHIP</td>
<td>136</td>
</tr>
<tr>
<td></td>
<td>Abstract</td>
<td>138</td>
</tr>
<tr>
<td></td>
<td>Introduction</td>
<td>139</td>
</tr>
<tr>
<td></td>
<td>Materials and methods</td>
<td>141</td>
</tr>
<tr>
<td></td>
<td>Results</td>
<td>151</td>
</tr>
<tr>
<td></td>
<td>Discussion</td>
<td>164</td>
</tr>
<tr>
<td></td>
<td>Conclusion</td>
<td>169</td>
</tr>
<tr>
<td></td>
<td>Acknowledgements</td>
<td>170</td>
</tr>
<tr>
<td></td>
<td>Supplementary section</td>
<td>171</td>
</tr>
<tr>
<td>8</td>
<td>General Discussion</td>
<td>176</td>
</tr>
<tr>
<td></td>
<td>Introduction</td>
<td>176</td>
</tr>
<tr>
<td></td>
<td>Understanding contemporary demography is key to accurate species distribution modelling</td>
<td>176</td>
</tr>
<tr>
<td></td>
<td>The consequences of habitat loss and protection</td>
<td>178</td>
</tr>
</tbody>
</table>
Landscape type influences dispersal.................................................................179
Habitat quality and the role of introduced species.........................................181
Adapting to a future of change and stress......................................................182
Conclusion......................................................................................................184
Appendix..........................................................................................................186
References.......................................................................................................193
Thesis summary

In Australia anthropogenic development has resulted in substantial loss and modification of natural habitats. This development has occurred most intensively around the continent’s southern and eastern coastal areas where fertile soils and climates appropriate for agriculture are located. Consequently, a diverse range of species found within this region frequently suffer from fragmented distributions that alter evolutionary processes and result in increased population structure and the erosion of genetic diversity. Augmenting the effect of habitat clearing and alteration, climate change is predicted to result in increasing temperature and decreasing rainfall in many regions of Australia. What makes anthropogenic climate change a major threat is that its impact will occur in ecosystems already suffering fragmentation and other perturbations associated with human activity.

This thesis seeks to characterise the molecular demography of the ground-dwelling southern scrub-robin (*Drymodes brunneopygia*), a species whose future is at risk from both habitat loss and climate change. I begin by reviewing the current use and potential role of molecular demography to inform species distribution modelling for conservation. My study of the southern scrub-robin itself begins with the development of microsatellites. Employing these microsatellites, I investigate genetic diversity and recent migration across intact and fragmented mallee vegetation in southern Australia. Our assessment of habitat protection for this species reveals that large areas of contiguous native vegetation are most often conserved toward the climatically extreme, northern distribution of the southern scrub-robin. Conversely, we find that genetic diversity and larger effective population size are concentrated in southern regions, which are dominated by agriculture.

Subsequently I investigate the composition and structure of different mallee understorey vegetation types, and the nature of their resources and risks to dispersing southern scrub-robins in both the historic (pre-clearing) and contemporary landscapes. Landscape types with an open or inaccessible understorey were shown to increase population genetic structure in the southern scrub-robin, in particular chenopod habitat. Conversely, landscape types that offered a dense, accessible understorey structure decreased genetic structuring, possibly due to increased predator protection and foraging.
opportunities during dispersal. I proceed by investigating the relationship between genetic diversity and habitat quality at southern scrub-robin home sites. Genetic diversity was diminished by the presence of feral predators and weed infestations, suggesting the control of invasive species should be a conservation priority for the southern scrub-robin. I also confirm the fundamental requirement of a dense shrubby understorey for this species, suggesting that control of feral herbivores may also be of conservation benefit.

Finally, I consider the role that adaptation to change can play in securing the future of the southern scrub-robin in an era of habitat loss and climate change. Simultaneously considering the effects of distance and the environment, I identify substrate and temperature conditions among the most important environmental variables associated with spatial patterns of genetic diversity. To prioritise regions for additional conservation actions, I consider predicted genetic uniqueness, land use, current and future habitat suitability and the amount of pressure existing genetic-climate relationships are expected to experience.
Declaration of Authorship

This work contains no material which has been accepted for the award of any other degree or diploma in any university or other tertiary institution to Jolene Scoble and, to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference has been made in the text. I give consent to this copy of my thesis when deposited in the University Library, being made available for loan and photocopying, subject to the provisions of the Copyright Act 1968. The author acknowledges that copyright of published works contained within this thesis (as listed below) resides with the copyright holder(s) of those works.

Published works contained within this thesis:


I also give permission for the digital version of my thesis to be made available on the web, via the University’s digital research repository, the Library catalogue, the Australasian Digital Theses Program (ADTP) and also through web search engines, unless permission has been granted by the University to restrict access for a period of time.

Jolene Scoble
August 2012

Cover photo: Drymodes brunneopygia (southern scrub-robin). Photo courtesy of Matt Goulton.
Thesis acknowledgements

Completion of this thesis would not have been possible without the support of my many supervisors. Thank you to Andy Lowe for assisting with my difficult transition to molecular biologist, and helping me to become a more independent and confident scientist; to Mike Gardener for his time, patience and knowledge around molecular lab work and analyses, to Anita Smyth for her constant confidence in me and modelling expertise; to Leo Joseph for his keen interest in helping me develop my writing style; and to Peter Cale for being my sounding board in the field and helping me to not take myself too seriously.

Special thanks are also in order to some collaborators on my PhD. Wally Klau’s mentorship around bird capture and banding enabled me to obtain my student license and work independently. Nigel Willoughby from the Department of Environment and Natural Resources helped me find my feet both in the Murray Mallee and with the southern scrub-robin. Kathy Saint from the University of Adelaide, Alison Fitch from Flinders University and Ralph Foster from the Museum of South Australia were all incredibly supportive of me in the lab. Bert Harris from the University of Adelaide was an immense help to me with his never-ending patience and cheerfulness throughout our modelling collaboration. Kristen Williams from CSIRO was a knowledgeable and patient collaborator with my last modelling manuscript toward the end of my PhD, when time was of the essence.

I would also like to thank my fellow PhD students, whose friendship, skills and knowledge were always available to me, and made my PhD such a positive experience. I would like to make particular mention of my fantastic and ever supportive lab group, especially those who shared my corner of the office, Elly Dormontt and Martin Breed, and also Fran (Phyllis) MacGillivray. To the ladies who lunched, Kym Abrams and Christina Adler, and the many people who eventually joined us, thank you for making the Darling building a more social and friendly place.

This project would have been impossible without the generous funding made available by CSIRO (Climate Adaptation Flagship), Department of Environment and Natural Resources in South Australia.
(Wildlife Conservation Fund), Sir Mark Mitchell Research Foundation, Birds Australia (Stuart Leslie Bird Research Award) and Australian Geographic Society. I would also like to thank the many organisations and people who welcomed me onto their properties, including Calperum and Taylorville sanctuaries (Australian Landscape Trust), Gluepot Reserve (Birds Australia), Yookamurra and Mt Gibson sanctuaries (Australian Wildlife Conservancy), Brookfield conservation park (Conservation Volunteers Australia), and the many reserves cared for by the Department of Environment and Natural Resources, South Australia and Department of Environment and Conservation, Western Australia.

Lastly, I would like to acknowledge all my volunteers for giving their time so generously to my make project a reality. In particular I would like to thank Matthew Goulton, the one volunteer silly enough to stick around and become my husband. You were my hero during the good times and the tough times alike, and gave me the encouragement and support I needed to see this PhD through to the end.
Chapter 1:

General Introduction

Human impacts: habitat change and loss

The exponential growth of the human race over recent centuries has brought about an enormous, corresponding loss of natural ecosystems in the wake of expanding areas of agriculture and urbanisation. An astounding 40% of net terrestrial ecosystem productivity is now appropriated for human use (Vitousek et al. 1986), with 16 million square kilometres of cropland (Ramankutty and Foley 1999) and 33 million square kilometres of grazing under production (Asner et al. 2004). In Australia, 61.5% of land is used for agricultural purposes (Beeton 2006). Clearing has reduced native vegetation cover to 86.6% of that prior to European settlement of Australia, however this figure masks a high level of modification and degradation present in remaining regions (Beeton 2006). Some 39% of Australia’s bioregions have greater than 30% of their total ecosystems threatened, predominately from land clearing (Sattler 2002). Such statistics leave little doubt that loss of native habitat, both in Australia and worldwide is the greatest ongoing threat to biodiversity (Fahrig 2003, Bennett et al. 2006). While the exact rate of species extinction in different taxa or regions, let alone globally, is a contentious and ongoing debate, scientists agree that current extinction rates greatly exceed typical background levels of species loss (Stork 2010). Australia alone has lost some 56 species to extinction since European settlement, and the existence of another 388 is currently considered threatened (Department of Sustainability 2009).

Habitat loss has a cascade of effects on species’ demography that in many cases decreases population size, and in some cases, leads to extinction. Amount of habitat is considered the dominant driver of species occurrence, and hence species richness (e.g. Radford et al. 2005). The habitat for a species may be defined as a suite of environmental resources and conditions that enable it to survive and reproduce. While the term habitat has been synonymous with a particular vegetation association or simply native vegetation itself, this definition fails to recognise that many species require several different vegetation types to survive and/or reproduce (Smyth and Pavey 2001), and that the
agricultural matrix may provide for some or all of a species’ requirements (Hall et al. 1997, Bennett et al. 2006). Furthermore, a definition of habitat based on vegetation alone does not distinguish interspecific differences in environmental requirements, nor recognise intraspecific gradients of environmental suitability (Fischer and Lindenmayer 2007). While native vegetation does not equate to a species-specific definition of habitat, the loss of native vegetation does often result in the loss of many species habitats, with serious ramifications for species persistence.

When the extent of available habitat decreases due to anthropogenic clearance, the amount and/or diversity of resources available to species also diminishes, reducing the carrying capacity of remaining habitat and hence population size of resident species (Bennett et al. 2006, Fletcher Jr et al. 2007). If the amount of habitat falls below a critical threshold it may preclude occupancy all together (e.g. Singer et al. 2001). Smaller patch size is also likely to contribute indirectly to decreasing population size via the choices of dispersing individuals. Small habitat patches may have lower rates of immigration if conspecific attraction, whereby dispersing individuals are attracted to settle at new home site on the basis of conspecific presence, is stronger in larger patches due to large population size (Fletcher 2006). Small habitat patches may also struggle to retain individuals as the chance of encountering a habitat boundary is greater when compared to a larger patch, increasing relative emigration rates (Bowman et al. 2002). Decreasing the amount of habitat also increases the isolation of given habitat patch, inhibiting the movement of individuals between patches on a daily basis (e.g. foraging), as well as the dispersal of juveniles (Fischer and Lindenmayer 2007). Finally, some predators occur in higher densities or spend more time in small patches (the enemies hypothesis; Root 1973). Individuals existing in small, agriculturally embedded habitat patches may have a heightened chance of predation and/or decreased reproductive success (Pita et al. 2009, Arthur et al. 2010). The cumulative effect of decreasing population size is heightened susceptibility to chance events that could result in local extirpation (Bennett et al. 2006).

Anthropogenic clearance of native vegetation from a landscape also changes the composition of landscape elements and the relative amount of each (Bennett et al. 2006). This can refer to a decrease in, or total loss of, a particular vegetation association (e.g. hummock woodlands), or some
aspect of vegetation composition (e.g. hummock grasses) or structure (e.g. ground cover) (Bennett et al. 2006, Johnson et al. 2007). Changes to the landscape resulting from agriculture also add to the collection of landscape elements (such as crops and dams) available to resident species and increase habitat suitability for some, while decreasing it for others (e.g. Clarke et al. 2001). Landscape composition influences the occurrence of species through the availability of necessary resources that constitute their habitat. For some species, habitat is comprised of several landscape elements that provide resources for different facets of their life-history, such as breeding and feeding. Parrot species may feed and roost or nest in different vegetation types (Amuno et al. 2007), or move seasonally between areas to track resources (Stahala 2008). Some mosaic elements may have a disproportionately large impact on species distributions, such as riparian habitats (Johnson and Stinchcombe 2007). Habitat heterogeneity is a key predictor of species richness in agricultural landscape mosaics, with both natural and anthropogenic landscape elements contributing to biodiversity (Haslem and Bennett 2008). However species diversity counts all species, common or threatened, as equal and may not give an accurate indication of the conservation value of a landscape (Bennett et al. 2006).

Anthropogenic clearing often fragments the formerly contiguous habitat of a given species (Fahrig 2003). Habitat fragmentation refers to the spatial configuration (as distinct from the amount) of landscape elements which constitute a species habitat, and may occur naturally or due to anthropogenic activities. Several emergent properties of fragmented habitat are important to species’ demography. Subdivision describes the degree of habitat fragmentation and the resulting number of habitat patches (Bennett et al. 2006). Subdivision influences patch size, amount of edge and the distance between patches, and is correlated with the amount of vegetation in the landscape (Fahrig 2003). The degree of aggregation of habitat describes the proximity of patches, and will be of particular importance to species with limited dispersal, or when habitat patches are fragmented by landscape elements that impede dispersal between them (Bennett et al. 2006). Physical continuity of landscape elements that form a species’ habitat is related to both habitat amount and aggregation, and may also be influenced by patch shape (Bennett et al. 2006). A study of blue-breasted fairy-wrens *Malurus pulcherrimus* found that smaller habitat patches had greater reproductive success because
they could not support Horsfield’s bronze-cuckoo, a specialist brood parasite of the wrens (Brooker and Brooker 2002). However juveniles were 14% less likely to die during dispersal in well-connected patches (Brooker and Brooker 2002).

Habitat loss and fragmentation have particularly important implications for species demography, and consequently, intraspecific genetic diversity. Species suffering from shrinking population size and increasingly fragmented distributions are susceptible to altered evolutionary processes, including decreased gene flow among the metapopulation, coupled with increasing genetic drift and increased levels of inbreeding (Stow et al. 2001, Schmuki et al. 2006, Walker et al. 2008, Pavlacky et al. 2009). The increases in population structure and the erosion of genetic diversity as a result leave species susceptible to local extirpation due to disease, predation, climatic extremes and chance events, and constrain future adaptive capacity. Understanding and managing genetic diversity in the face of habitat loss and fragmentation is playing an increasingly important role in conservation (Hendry et al. 2011).

**Human impacts: climate change**

Human activities have not only had a profound effect on the physical environment, our actions are also causing unprecedented changes in the climate. Proof of climate warming is now unequivocal. Reporting by the 2007 Intergovernmental Panel on Climate Change (IPCC) indicates that the linear warming trend in the 50 years to 2005 is almost twice that of the 100 year period to 2005 (IPCC 2007a). Concomitantly, decreasing snow and ice extent and an increasing sea level are all consistent with global warming (IPCC 2007a). The same report also places high confidence in the cause of the global warming trend: human activities. Fossil fuel use and anthropogenic-driven land use change have contributed to increasing levels of atmospheric greenhouse gases that far exceed natural levels. Greenhouse gas emissions since the inception of the industrial era (~1750) have predominately been responsible for a sharp rise in radiative forcing unparalleled in the last 10,000 years (IPCC 2007a). Between 1970 and 2004 alone there was a 70% increase in the emission of greenhouse gases, principally due to energy supply, transport and industry (IPCC 2007a). Without the increase in
greenhouse gasses emissions and subsequent depletion of the stratospheric ozone layer, solar and volcanic forcings would likely have cooled the climatic system (IPCC 2007a). The effects of anthropogenic forcing reach beyond average temperature; they are associated with increasing temperature extremes, the risk of heat waves, tropical cyclone activity, the area of land affected by drought and the frequency of heavy precipitation events (IPCC 2007a).

The IPCC (2007a) also reports that there is now strong evidence for an effect of anthropogenically forced climate change on terrestrial, freshwater and marine ecosystems. Climate change may be expected to act on biota in four different ways (Hughes 2000). Altered environmental conditions may act directly on physiological processes such as metabolism in animals, or photosynthesis in plants (Hughes 2000, Acevedo-Whitehouse and Duffus 2009, Walck et al. 2011). The distribution of species may change as they track their climatic envelope either latitudianally or via increasing elevation, altering species interactions and ecosystem composition (Hughes 2000, Root et al. 2003, Sekercioglu et al. 2008, Thomas 2010). The timing and duration of phenological events, where cues are environmental, may be altered, and species interaction based on phenology may be disrupted (Hughes 2000, Root et al. 2003, Carey 2009, Hegland et al. 2009, Miller-Rushing et al. 2010). Lastly, some species may undergo in situ adaptation to altered environmental conditions (Hughes 2000, Reusch and Wood 2007)

In marine ecosystems, ocean acidification is considered the primary threat to biodiversity. Rising concentrations of carbon dioxide in the atmosphere have led to increased levels of seawater carbon dioxide, altering oceanic carbonate chemistry and decreasing pH levels (Gattuso and Buddemeier 2000). Importantly, the deposition and dissolution of calcium carbonate is at threat from altered carbonate chemistry (Gattuso and Buddemeier 2000), impeding the process of calcification in marine organisms such as reef-building corals, with negative consequences for their growth, reproduction and survival (Kroeker et al. 2010). In freshwater systems, climate change is projected to alter thermal regimes and biogeochemical processes, with implications for aquatic productivity, food webs, and species demography and biodiversity (Wrona et al. 2006). Locally adapted Arctic and Antarctic species are expected to be at greatest threat from extinction, while other species may shift
their distributions via poleward flowing river systems (Wrona et al. 2006, Thomas 2010). Nutrient and carbon enrichment as a result of increased permafrost thawing and enhanced productivity is also likely to alter freshwater carbon chemistry, and hence the carbon source/sink nature of water bodies (Wrona et al. 2006).

Terrestrial ecosystems find themselves in no less danger than their aquatic counterparts. Invasive species may have increased opportunities for successful establishment and range expansion under a warming climate (Walther et al. 2009). Empirical studies have demonstrated that native species’ ranges are overwhelmingly shifting toward the poles, and in topographically diverse regions, upslope to higher elevations (Root et al. 2003, Thomas 2010). Montane species are frequently assumed to be at greatest threat as their climatic envelope has the potential to disappear off the top of the mountain (Shoo et al. 2005, 2006), and in some instances they may be unable to migrate latitudinally through the warmer valleys to climatic refugia (Hilbert et al. 2004). However bioclimatic modelling suggests that flatland fauna may be at equal or even great risk from climate change. While both montane and flatland species may experience reduced range size with increasing temperature, flatland species may have to track their climatic envelope shifts latitudinally over a large distance (Peterson et al. 2002, Peterson 2003). A 3°C increase in temperature necessitates a shift of 500 m in elevation, or 300-400 km in latitude in the temperate zone (Hughes 2000). Additionally, the topography of montane habitats has afforded them greater protection from the fragmentation prevalent in flatland habitats due by agriculture and urbanisation, which creates barriers to effective dispersal as species attempt to track their climatic envelope (Hannah et al. 2002).

Climate change is also altering environmentally-cued phenology in terrestrial ecosystems, with important implications for species interactions. Changes to temperature and water availability are likely to be critical to the survival, dormancy and germination of seeds, and may compromise the emergence and vigour of seedlings (Walck et al. 2011). Increased levels of carbon dioxide have a fertilization effect on many plant species, increasing growth (e.g. Atkin et al. 1999). Temperature changes (amongst others) have altered the onset of plant reproductive cycles and the emergence of pollinators, with the potential for phenological desynchronisation to occur (Hegland et al. 2009,
Conservation in a brave new world

Anthropogenically-forced climatic change is having far reaching effects on natural ecosystems around the globe, many of which may compromise species survival. While climate change is hardly a new phenomenon, anthropogenic climate change is a major threat to biodiversity as it is occurring at a rate unprecedented in recent history, and its impact will occur in ecosystems already suffering fragmentation and other perturbations associated with human activities (Mackey et al. 2008). Conservation strategies that emphasise climate change adaptation have focussed on the role protected areas can play in supporting species during range shifts, by increasing the amount and connectivity of protected lands, and by conserving areas best able to protect biodiversity as the climate changes (Hannah et al. 2002, Hannah et al. 2007, Hannah 2008, Vos et al. 2008, Hannah 2010). National protected area systems may fail to support species range shifts without cross border collaboration. Partnerships among neighbouring countries will be necessary to develop appropriate international protection area complexes (Hannah 2010).

Agricultural areas are also likely to have increasing conservation demands placed upon them due to climate change. Existing protected areas were preferentially set up in regions that were unsuitable for agriculture or urbanisation, rather than on the basis of inherent biological value, such that many ecosystems and resident species are already underrepresented by the reserve system (Fuller et al. 2010). This situation may be exacerbated by climate change, as species experience range shift. Understanding and improving the ability of the species to disperse through and survive in such agricultural systems is likely to become the cornerstone of many future conservation efforts (Hannah et al. 2002, Hannah et al. 2007, Hannah 2008, Vos et al. 2008). Preparing agricultural and urban regions for an increased role in the conservation of biodiversity requires substantial forward planning. Restoration activities require not only knowledge gathering around the demography of
affected species, but also land acquisition or landholder agreements for replanting or improving tracts of native vegetation (Hannah et al. 2002). The growth and development of these ecosystems will require substantial time before they can fulfil their role as habitat and dispersal corridors for biodiversity into the future.

Conservation strategies developed in response to climate change pressures are also increasingly recognising that in addition to patterns of biodiversity, there is a need to consider and preserve the processes that generate biodiversity and will enable adaption to new conditions. In the past, preserving current patterns of biodiversity and preventing future loss, or attempting to recreate patterns that existed prior to modern human urbanisation and agriculture, has been the goal of conservation plans (Dunlop 2008). This goal is at odds with preserving evolutionary processes, which both generates new species and results in the loss of others (Mace and Purvis 2008). Incorporating processes into conservation planning has long proved a challenge for policy makers and conservation managers, for whom visible, pattern based conservation outcomes are more easily justified to the public over the often slow and indiscernible outcomes of evolutionary processes (Mace and Purvis 2008). Furthermore, information regarding the spatial patterns of biodiversity is more readily available and easily synthesized, compared with often incomplete, complex information regarding process (Smith et al. 1993).

Despite the challenges of considering processes that generate biodiversity, their inclusion in conservation planning is critical (Hendry et al. 2011, Lankau et al. 2011, Sgro et al. 2011). Most biota have evolved in a climate that has over time had substantial oscillations (Byrne 2008b, Mackey et al. 2008) and consequently many species exhibit adaptations to climatic change (Soule et al. 2004). Standing genetic variation in key traits resulting from a species evolutionary history under past climate change will in some instances enable a quick response to contemporary climate change via phenotypic diversity and plasticity (Hendry et al. 2011, Lankau et al. 2011). If the current phenotypic distribution does not enable a species to persist under changed climatic conditions, intraspecific genetic diversity may facilitate in situ adaptation. This may be a particularly important response for species with low mobility that are unlikely to successfully track shifts in their climatic
envelope, especially through fragmented habitats (Sgro et al. 2011). Genetic diversity and consequently, adaptive potential, can be protected by facilitating gene flow among populations to maintain large effective (breeding) population sizes that avoid inbreeding and drift (Mace and Purvis 2008, Hendry et al. 2011, Sgro et al. 2011). Conservation strategies that seek to increase connectivity among reserves to enable range shifts will also help to maintain high levels of gene flow necessary for sustaining genetic diversity (Sgro et al. 2011). Environmental gradients that generate and maintain genetic diversity in the landscape are also frequently excellent surrogates for conservation planning (Davis et al. 2008, Thomassen et al. 2010).

A model species: the southern scrub-robin

There are several factors that may predispose a species to increased threat from habitat loss and/or climate change. Species whose distributions substantially intersect agricultural and/or urban areas are more likely to suffer from decreased population size, increased population structure and the erosion of genetic diversity (Stow et al. 2001, Schmuki et al. 2006, Walker et al. 2008, Pavlacky et al. 2009). These species are also poorly placed to respond successfully to novel threats such as climate change if low levels of genetic diversity preclude in situ adaption (Hendry et al. 2011, Sgro et al. 2011). Species that live in flat regions may be more at risk from habitat loss as the topography is more conducive to agriculture and urbanisation (Hannah et al. 2002), and will have to travel over greater distances to track their climate envelope compared to species able to move upslope (Hughes 2000). Species with specific habitat requirements are less likely to successfully locate appropriate habitat following habitat loss or climate change that necessitates a range shift. Ground-dwelling species are also particularly at threat from habitat degradation and clearance, because habitat changes frequently occur first, and most radically at the ground level (Ford et al. 2001). Those species that have low mobility may struggle to move away from areas of habitat destruction and maintain gene flow across agricultural and urban regions, and could be unable to track a shifting climate envelope (Reid and Fleming 1992, Ford et al. 2001).
The southern scrub-robin (*Drymodes brunneopygia*) is a ground dwelling avian species whose life history attributes place it at increased risk from threats such as habitat loss and climate change. The southern scrub-robin is a sedentary, territorial passerine species endemic to the mallee region of southern Australia (Higgins and Peter 2002). The term *mallee* is an Australian Aboriginal word referring to the eucalypt growth habit typified by low shrubby trees or tall shrubs with a multi-stemmed lignotuber (Specht 1981, Hill 1989). Mallee communities change in understorey from heath through to chenopodiaceous vegetation and then hummock grassland with increasing aridity (Specht 1981), although the southern scrub-robin is generally confined to mallee habitat comprised of shrubby understorey (Higgins and Peter 2002). Mallee communities occur in areas receiving between 250 mm and 450 mm average annual rainfall and are thus classified as semi-arid (Sparrow 1989). Agricultural practices within the mallee have been responsible for dramatic changes to ecosystem structure and function. In Western Australia, the Wheatbelt, as its name suggests, was predominately cleared in the 1900’s for wheat cropping. Around 36% was cleared by 1920, and by 1984 clearing had peaked at 93% (Prober and Smith 2009). In South Australia toward the east of the scrub-robin’s distribution lies the Murray Mallee region, which covers an area of 18,360 km² south of the Murray River, of which only 20% (3,660 km²) remains as remnant vegetation (Willoughby 2006). This is largely due to clearing for broad acre cropping. Grazing by livestock in the mallee since the 1850’s and the introduction of rabbits and goats has also altered vegetative structure, composition and ground cover, especially at areas of high use such as water points (Reid and Fleming, Landsberg 1997, Harrington 2002).

The scrub-robin’s life history is intimately dependent on the health of ground habitat: it searches for food within the litter layer (invertebrates and seeds), nests on or close to the ground, and is heavily reliant on low shrubs for camouflage from mammalian and avian predators (Higgins and Peter 2002). Unlike many other avian species adapted to arid conditions, it lays a clutch of only one egg and appears unable to increase this number when conditions are favourable, and has a low annual fledgling production rate (Brooker 2001). The southern-scrub robin is known to avoid using, and nesting near, human-made habitat edges, which may increase levels of predation (Luck et al. 1999),
and it decreases in abundance where grazing has diminished vegetative ground cover (Harrington 2002, Cale and Mladovan 2007). It is unsurprising then, that sedentary, ground dwelling species are considered disproportionately threatened compared to birds with different life histories in arid and semi-arid habitats (Reid and Fleming 1992). While the scrub-robin is listed as of least concern (The Action Plan for Australian Birds 2000 (Garnett and Crowley 2000)) populations are disappearing from fragments and the species has a decreasing area of occupancy (Garnett and Crowley 2000).

![Figure 1.1. Current distribution of the southern scrub-robin (Drymodes brunneopygia)](Schodde and Mason 1999)

The impact of climate change has already begun to alter the distributional range of a substantial number of avian species already contending with habitat fragmentation (Hughes 2000, Root et al. 2003). The low reproductive rate, sedentary nature and ground-dwelling life history could make the scrub-robin highly susceptible to any changes in distribution range that may be induced by climatic
change. Forecast temperature increases may force scrub-robins to navigate habitat remnants in order to locate isolated climatic refugia. A definitive understanding of the habitat requirements and dispersal ability of the southern scrub-robin is urgently needed to in order for managers to prevent further population declines and ensure this species’ persistence in the face of climate change.

**Project Objectives**

We will undertake a genetic analysis of the southern scrub-robin to elucidate metapopulation structure, and understand historical and contemporary dispersal across ecotones between intact and relictual mallee vegetation. Using this information, we aim to inform future conservation guidelines for this species to mitigate the effects of both habitat loss and climate change.

Our objectives are:

1. Characterise the effect of habitat loss on population structure and genetic diversity within the metapopulation
2. Understand historical and contemporary dispersal dynamics of selected populations to in relation to land cover type;
3. Describe the “habitat envelope” of the southern scrub-robin, a species sensitive to climate change, at sites of intact and relictual mallee vegetation;
4. Using our understanding of the habitat envelope and demographic dynamics of the southern scrub-robin, identify new management guidelines that maintain high genetic diversity and facilitate adaptation to climate change and other novel threats.
Chapter 2:

A case for incorporating phylogeography and landscape genetics into species distribution modelling approaches to improve climate adaptation and conservation planning

Jolene Scoble\textsuperscript{1,2} and Andrew John Lowe\textsuperscript{1,3*}

\textsuperscript{1} Australian Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Science University of Adelaide, North Terrace, SA 5005, Australia.

\textsuperscript{2} CSIRO, Climate Adaptation Flagship, GPO Box 1700, Canberra, ACT 2601, Australia.

\textsuperscript{3} State Herbarium of South Australia, Science Resources Centre, Department for Environment and Heritage, Adelaide, SA 5005, Australia.

*Corresponding author: andrew.lowe@adelaide.edu.au

Running head: Incorporating molecular marker information into species modelling

Article type: Biodiversity review
STATEMENT OF AUTHORSHIP

A case for incorporating phylogeography and landscape genetics into species distribution modelling approaches to improve climate adaptation and conservation planning

This chapter has been published in: Diversity and Distributions – 2010, 16(3), 343-353.

**Jolene Scoble**
Conceived ideas, searched and collated literature, completed all data analysis, and prepared manuscript as principle author.

Signed:  
Date: 27/01/2012

**Andrew John Lowe**
Conceived ideas, and helped write manuscript.

Signed:  
Date: 30/01/2012
Permission to reprint

This is a License Agreement between jolene scoble ("You") and John Wiley and Sons ("John Wiley and Sons") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by John Wiley and Sons, and the payment terms and conditions.

All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

<table>
<thead>
<tr>
<th>License Number</th>
<th>2832780844934</th>
</tr>
</thead>
<tbody>
<tr>
<td>License date</td>
<td>Jan 19, 2012</td>
</tr>
<tr>
<td>Licensed content publisher</td>
<td>John Wiley and Sons</td>
</tr>
<tr>
<td>Licensed content publication</td>
<td>Diversity and Distributions</td>
</tr>
<tr>
<td>Licensed content title</td>
<td>A case for incorporating phylogeography and landscape genetics into species distribution modelling approaches to improve climate adaptation and conservation planning</td>
</tr>
<tr>
<td>Licensed content author</td>
<td>Jolene Scoble, Andrew John Lowe</td>
</tr>
<tr>
<td>Licensed content date</td>
<td>May 1, 2010</td>
</tr>
<tr>
<td>Start page</td>
<td>343</td>
</tr>
<tr>
<td>End page</td>
<td>353</td>
</tr>
<tr>
<td>Type of use</td>
<td>Dissertation/Thesis</td>
</tr>
<tr>
<td>Requestor type</td>
<td>Author of this Wiley article</td>
</tr>
<tr>
<td>Format</td>
<td>Print and electronic</td>
</tr>
<tr>
<td>Portion</td>
<td>Full article</td>
</tr>
<tr>
<td>Will you be translating?</td>
<td>No</td>
</tr>
<tr>
<td>Order reference number</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>0.00 USD</td>
</tr>
</tbody>
</table>

TERMS AND CONDITIONS

This copyrighted material is owned by or exclusively licensed to John Wiley & Sons, Inc. or one of its group companies (each a "Wiley Company") or a society for whom a Wiley Company has exclusive publishing rights in relation to a particular journal (collectively WILEY). By clicking "accept" in connection with completing this licensing transaction, you agree that the following terms and conditions apply to this transaction (along with the billing and payment terms and conditions established by the Copyright Clearance Center Inc., ("CCC’s Billing and Payment terms and conditions"), at the time that you opened your Rightslink account (these are available at any time at http://myaccount.copyright.com).

Terms and Conditions

1. The materials you have requested permission to reproduce (the "Materials") are protected by copyright.

2. You are hereby granted a personal, non-exclusive, non-sublicensable, non-transferable, worldwide, limited license to reproduce the Materials for the purpose specified in the licensing process. This license is for a one-time use only with a maximum distribution equal to the number that you identified in the licensing process. Any form of republication granted by this licence must be completed within two years of the date of the grant of this licence (although copies prepared before may be distributed thereafter). The Materials shall not be used in any other manner or for
any other purpose. Permission is granted subject to an appropriate acknowledgement given to the author, title of the material/book/journal and the publisher. You shall also duplicate the copyright notice that appears in the Wiley publication in your use of the Material. Permission is also granted on the understanding that nowhere in the text is a previously published source acknowledged for all or part of this Material. Any third party material is expressly excluded from this permission.

3. With respect to the Materials, all rights are reserved. Except as expressly granted by the terms of the license, no part of the Materials may be copied, modified, adapted (except for minor reformatting required by the new Publication), translated, reproduced, transferred or distributed, in any form or by any means, and no derivative works may be made based on the Materials without the prior permission of the respective copyright owner. You may not alter, remove or suppress in any manner any copyright, trademark or other notices displayed by the Materials. You may not license, rent, sell, loan, lease, pledge, offer as security, transfer or assign the Materials, or any of the rights granted to you hereunder to any other person.

4. The Materials and all of the intellectual property rights therein shall at all times remain the exclusive property of John Wiley & Sons Inc or one of its related companies (WILEY) or their respective licensors, and your interest therein is only that of having possession of and the right to reproduce the Materials pursuant to Section 2 herein during the continuance of this Agreement. You agree that you own no right, title or interest in or to the Materials or any of the intellectual property rights therein. You shall have no rights hereunder other than the license as provided for above in Section 2. No right, license or interest to any trademark, trade name, service mark or other branding ("Marks") of WILEY or its licensors is granted hereunder, and you agree that you shall not assert any such right, license or interest with respect thereto.

5. NEITHER WILEY NOR ITS LICENSORS MAKES ANY WARRANTY OR REPRESENTATION OF ANY KIND TO YOU OR ANY THIRD PARTY, EXPRESS, IMPLIED OR STATUTORY, WITH RESPECT TO THE MATERIALS OR THE ACCURACY OF ANY INFORMATION CONTAINED IN THE MATERIALS, INCLUDING, WITHOUT LIMITATION, ANY IMPLIED WARRANTY OF MERCHANTABILITY, ACCURACY, SATISFACTORY QUALITY, FITNESS FOR A PARTICULAR PURPOSE, USABILITY, INTEGRATION OR NON-INFRINGEMENT AND ALL SUCH WARRANTIES ARE HEREBY EXCLUDED BY WILEY AND ITS LICENSORS AND WAIVED BY YOU.

6. WILEY shall have the right to terminate this Agreement immediately upon breach of this Agreement by you.

7. You shall indemnify, defend and hold harmless WILEY, its Licensors and their respective directors, officers, agents and employees, from and against any actual or threatened claims, demands, causes of action or proceedings arising from any breach of this Agreement by you.

8. IN NO EVENT SHALL WILEY OR ITS LICENSORS BE LIABLE TO YOU OR ANY OTHER PARTY OR ANY OTHER PERSON OR ENTITY FOR ANY SPECIAL, CONSEQUENTIAL, INCIDENTAL, INDIRECT, EXEMPLARY OR PUNITIVE DAMAGES, HOWEVER CAUSED, ARISING OUT OF OR IN CONNECTION WITH THE DOWNLOADING, PROVISIONING, VIEWING OR USE OF THE MATERIALS REGARDLESS OF THE FORM OF ACTION, WHETHER FOR BREACH OF CONTRACT, BREACH OF WARRANTY, TORT, NEGLIGENCE, INFRINGEMENT OR OTHERWISE (INCLUDING, WITHOUT LIMITATION, DAMAGES BASED ON LOSS OF PROFITS, DATA, FILES, USE, BUSINESS OPPORTUNITY OR CLAIMS OF THIRD PARTIES), AND WHETHER OR NOT THE PARTY HAS BEEN ADVISED OF THE POSSIBILITY OF SUCH DAMAGES. THIS LIMITATION SHALL APPLY NOTWITHSTANDING ANY FAILURE OF ESSENTIAL PURPOSE OF ANY LIMITED REMEDY PROVIDED HEREIN.

9. Should any provision of this Agreement be held by a court of competent jurisdiction to be illegal, invalid, or unenforceable, that provision shall be deemed amended to achieve as nearly as possible the same economic effect as the original provision, and the legality, validity and enforceability of the remaining provisions of this Agreement shall not be affected or impaired thereby.

10. The failure of either party to enforce any term or condition of this Agreement shall not constitute a waiver of either party’s right to enforce each and every term and condition of this Agreement. No breach under this agreement shall be deemed waived or excused by either party unless such waiver or consent is in writing signed by the party granting such waiver or consent. The waiver by or consent of a party to a breach of any provision of this Agreement shall not operate or be construed as a waiver of or consent to any other or subsequent breach by such other party.

11. This Agreement may not be assigned (including by operation of law or otherwise) by you without WILEY’s prior written consent.

12. Any fee required for this permission shall be non-refundable after thirty (30) days from
receipt.

13. These terms and conditions together with CCC's Billing and Payment terms and conditions (which are incorporated herein) form the entire agreement between you and WILEY concerning this licensing transaction and (in the absence of fraud) supersedes all prior agreements and representations of the parties, oral or written. This Agreement may not be amended except in writing signed by both parties. This Agreement shall be binding upon and inure to the benefit of the parties' successors, legal representatives, and authorized assigns.

14. In the event of any conflict between your obligations established by these terms and conditions and those established by CCC's Billing and Payment terms and conditions, these terms and conditions shall prevail.

15. WILEY expressly reserves all rights not specifically granted in the combination of (i) the license details provided by you and accepted in the course of this licensing transaction, (ii) these terms and conditions and (iii) CCC's Billing and Payment terms and conditions.

16. This Agreement will be void if the Type of Use, Format, Circulation, or Requestor Type was misrepresented during the licensing process.

17. This Agreement shall be governed by and construed in accordance with the laws of the State of New York, USA, without regards to such state's conflict of law rules. Any legal action, suit or proceeding arising out of or relating to these Terms and Conditions or the breach thereof shall be instituted in a court of competent jurisdiction in New York County in the State of New York in the United States of America and each party hereby consents and submits to the personal jurisdiction of such court, waives any objection to venue in such court and consents to service of process by registered or certified mail, return receipt requested, at the last known address of such party.

Wiley Open Access Terms and Conditions

All research articles published in Wiley Open Access journals are fully open access: immediately freely available to read, download and share. Articles are published under the terms of the Creative Commons Attribution Non Commercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes. The license is subject to the Wiley Open Access terms and conditions: Wiley Open Access articles are protected by copyright and are posted to repositories and websites in accordance with the terms of the Creative Commons Attribution Non Commercial License. At the time of deposit, Wiley Open Access articles include all changes made during peer review, copyediting, and publishing. Repositories and websites that host the article are responsible for incorporating any publisher-supplied amendments or retraction issued subsequently. Wiley Open Access articles are also available without charge on Wiley's publishing platform, Wiley Online Library or any successor sites.

Use by non-commercial users

For non-commercial and non-promotional purposes individual users may access, download, copy, display and redistribute to colleagues Wiley Open Access articles, as well as adapt, translate, text- and data-mine the content subject to the following conditions:

- The authors' moral rights are not compromised. These rights include the right of "paternity" (also known as "attribution" - the right for the author to be identified as such) and "integrity" (the right for the author not to have the work altered in such a way that the author's reputation or integrity may be impugned).
- Where content in the article is identified as belonging to a third party, it is the obligation of the user to ensure that any reuse complies with the copyright policies of the owner of that content.
- If article content is copied, downloaded or otherwise reused for non-commercial research and education purposes, a link to the appropriate bibliographic citation (authors, journal, article title, volume, issue, page numbers, DOI and the link to the definitive published version on Wiley Online Library) should be maintained. Copyright notices and disclaimers must not be deleted.
- Any translations, for which a prior translation agreement with Wiley has not been agreed, must prominently display the statement: "This is an unofficial translation of an article that appeared in a Wiley publication. The publisher has not endorsed this translation."
Use by commercial "for-profit" organisations

Use of Wiley Open Access articles for commercial, promotional, or marketing purposes requires further explicit permission from Wiley and will be subject to a fee. Commercial purposes include:

- Copying or downloading of articles, or linking to such articles for further redistribution, sale or licensing;
- Copying, downloading or posting by a site or service that incorporates advertising with such content;
- The inclusion or incorporation of article content in other works or services (other than normal quotations with an appropriate citation) that is then available for sale or licensing, for a fee (for example, a compilation produced for marketing purposes, inclusion in a sales pack);
- Use of article content (other than normal quotations with appropriate citation) by for-profit organisations for promotional purposes;
- Linking to article content in e-mails redistributed for promotional, marketing or educational purposes;
- Use for the purposes of monetary reward by means of sale, resale, licence, loan, transfer or other form of commercial exploitation such as marketing products;
- Print reprints of Wiley Open Access articles can be purchased from: corporatesales@wiley.com

Other Terms and Conditions:

BY CLICKING ON THE "I AGREE..." BOX, YOU ACKNOWLEDGE THAT YOU HAVE READ AND FULLY UNDERSTAND EACH OF THE SECTIONS OF AND PROVISIONS SET FORTH IN THIS AGREEMENT AND THAT YOU ARE IN AGREEMENT WITH AND ARE WILLING TO ACCEPT ALL OF YOUR OBLIGATIONS AS SET FORTH IN THIS AGREEMENT.

v1.7

If you would like to pay for this license now, please remit this license along with your payment made payable to "COPYRIGHT CLEARANCE CENTER" otherwise you will be invoiced within 48 hours of the license date. Payment should be in the form of a check or money order referencing your account number and this invoice number RLNK500702737. Once you receive your invoice for this order, you may pay your invoice by credit card. Please follow instructions provided at that time.

Make Payment To:
Copyright Clearance Center
Dept 001
P.O. Box 843006
Boston, MA 02284-3006

For suggestions or comments regarding this order, contact RightsLink Customer Support: customercare@copyright.com or +1-877-622-5543 (toll free in the US) or +1-978-646-2777.

Gratis licenses (referencing $0 in the Total field) are free. Please retain this printable license for your reference. No payment is required.
A case for incorporating phylogeography and landscape genetics into species distribution modelling approaches to improve climate adaptation and conservation planning

Jolene Scobie1,2 and Andrew John Lowe1,3*

ABSTRACT

Aim We seek to demonstrate that whilst information derived from phylogeographic and landscape genetic approaches has been used broadly to further ecological and evolutionary hypothesis testing, it can also be used to further species modelling approaches, particularly where climatic and demographic methodologies are to be combined to tackle climate change adaptation and conservation planning.

Location General application.

Methods We start with a review of species distribution modelling studies that have used data derived from molecular marker studies, and identify which parameters can realistically be derived from molecular marker studies for inclusion in species and ecosystem distribution prediction and conservation planning.

Results We find that the uptake of phylogeographic and landscape genetic methods to inform species distribution modelling studies has to date been limited (particularly the latter approaches), despite offering clear potential to improve species modelling approaches that aim to combine climatic envelope and demographic parameters. Using a series of case studies, we demonstrate that phylogeographic approaches can be particularly useful for identifying biogeographic barriers and refugia, testing alternative demographic models, identifying concordant demographic patterns between species within a single ecosystem and testing temporal niche conservatism. We also find that landscape genetic approaches are particularly useful for quantifying landscape permeability and source/sink dynamics of meta-populations and identifying adaptive variation in the landscape. A summary of parameters that are derivable from such studies for modelling and conservation applications is provided.

Main conclusions Molecular marker methods have much to offer species distribution modeling, particularly in the field of climate adaptation. Molecular information can inform on species historical dynamics and contemporary demography necessary to advance species modelling paradigms that seek to integrate climatic and demographic drivers. Furthermore, recognizing diversity below species level and incorporating this information into modelling frameworks will enable conservation managers to plan for the capture of areas of evolutionary potential.

Keywords Climate change, landscape genetics, molecular markers, phylogeography, species distribution modelling.
INTRODUCTION

Recent and future predictions of climatic changes have important ramifications for the abundance, range, phenology and physiology of a substantial number of species (Hughes, 2000; Root et al., 2003; IPCC, 2007). In recognition of these issues, biodiversity conservation planning has shifted direction to align with new knowledge and community awareness about anthropogenically forced climate change (Rouget et al., 2006; Dunlop & Brown, 2008; Vandergeest et al., 2008; Vos et al., 2008). However, central to such a shift in ethos is the safeguarding of species distributions and the evolutionary processes maintaining species abundances and adaptational capacity (Klein et al., 2009), the uptake of which has, to date, been much slower for conservation planning and on-ground adaptation (Dunlop & Brown, 2008).

It also has been a difficult challenge for biologists to develop robust tools to develop biodiversity conservation planning for climate adaptation. Species distribution modelling, based predominantly on climate parameters, continues to lead the way (Beaumont & Hughes, 2002; Pearson & Dawson, 2003; Franklin, 2010). New advances in the field of species modelling and prediction have refined these tools by incorporating more sophisticated species parameters, such as meta-population demography and landscape interactions (Opdam & Waser, 2004; Keith et al., 2008; Vos et al., 2008), species life history traits (P0rry et al., 2008), species interactions (Araujo & Lusoto, 2007) and a consideration of evolutionary history (Rouget et al., 2003; Byrnes, 2008; Byrne et al., 2008).

In parallel, but to date in a largely separate literature, there have been significant advances in the application of molecular markers to understand population dynamics and historical demography (e.g. review by Sunnucks & Taylor, 2008). We believe that the lack of integration between these fields is potentially hindering progress to develop robust species distribution modelling approaches, particularly those which wish to progress beyond simple climatic envelope approaches and incorporate demographic processes.

In this article, we review recent literature to determine whether developments in molecular marker tools have been used frequently in species distribution modelling. We then outline, with case studies, the range of species and population parameters that can be derived from different molecular marker studies (mainly in the fields of phylogeography and landscape genetics, but also in the recently expanding area of adaptive variation screening). Finally, we attempt to give clear guidance on the most appropriate parameters, derivable from molecular marker approaches, for species distribution modelling and conservation planning, with a particular focus on climate adaptation.

THE USE OF MOLECULAR MARKER STUDIES IN SPECIES MODELLING APPROACHES

A species’ genome cannot only be used to inform on the impact of historical and contemporary demography and connectivity, but it also contains the raw material for species to adapt to future challenges (Lacy, 1987; Riddle et al., 2008). Species persistence under a changing climate is integrally tied to meta-population cohesion and adaptational capacity, which has also been shaped by historic environmental change and impacts on demography (Watts et al., 1998; Biddle et al., 2008). A number of molecular marker methods are available for such studies, and their appropriate application depends on the temporal and spatial scale of the study. A number of reviews have outlined in detail the appropriate application of a range of different marker types to phylogeographic, landscape genetic and adaptive gene studies (e.g. Lowe et al., 2004; Sunnucks & Taylor, 2008), which are summarized briefly in Table 1 and covered in more detail in the subsequent sections later.

Whilst recent developments in molecular marker approaches could have tremendous application for species modelling studies, in our experience, there has not been broad integration across these fields. To test this notion, we reviewed modelling studies, published between 2008 and July 2009, to investigate whether molecular marker data had been incorporated into a range of species distribution and demographic modelling studies (Fig. 1 and Appendix S1 in Supporting Information). It is clear from this literature survey that where they have been used, molecular marker methods have mainly been applied to understand and model species distributions under past climates (sometimes in lieu of a fossil record; e.g. Byrne, 2008). However, studies considering more contemporary distributions rarely utilized DNA information, and never did so when employing a bioclimatic model (Fig. 1; e.g. Keith et al., 2008).

It appears therefore that whilst phylogeographic parameters have been partially recognized for their potential to offer an independent data source for modelling historical species distributions, the use of contemporary population dynamic data derived from molecular marker studies has been much more limited.

Recent modelling studies have questioned the relative importance of climate in relation to species demography (Muotin et al., 2007; Davis et al., 1998; Pearson & Dawson, 2003; Araujo & Lusoto, 2007) and have highlighted the critical importance of incorporating life history attributes into modelling approaches to produce more realistic estimates of changed species distributions (Araujo & Lusoto, 2007; Keith et al., 2008). Thus, we strongly support the combined use of historical and contemporary population dynamic information derived from molecular marker studies in species distribution modelling approaches to help advance this developing field.

In the rest of this article we outline, with case studies, how approaches in the fields of phylogeography and landscape genetics can be applied to species modelling and planning for climate adaptation and conservation. In particular, we consider the application of phylogeographic approaches to the identification of biogeographic barriers and refugia, the testing of alternative demographic models, identification of concordant demographic patterns between species of a single ecosystem.
<table>
<thead>
<tr>
<th>Demographic parameter</th>
<th>Molecular approach to inform actions</th>
<th>Markers/information required</th>
<th>Scale</th>
<th>Modelling application</th>
<th>Relevance to conservation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location of long-term barriers to movement</td>
<td>Phylogeny</td>
<td>Organelle and nuclear DNA, appropriate paleoclimate</td>
<td>Regional/Continental</td>
<td>Distributional modelling</td>
<td>Will mediate a species’ ability to track a shifting climatic niche or reach refugia</td>
</tr>
<tr>
<td>Location of former barriers to movement/hybrid zones</td>
<td>Phylogeny</td>
<td>Organelle and nuclear DNA, appropriate paleoclimate</td>
<td>Regional/Continental</td>
<td>Distributional modelling</td>
<td>Hybrid zones are often locations of novel genetic combinations that may facilitate evolution</td>
</tr>
<tr>
<td>Location of long-term refugia</td>
<td>Phylogeny</td>
<td>Organelle and nuclear DNA, appropriate paleoclimate</td>
<td>Regional/Continental</td>
<td>Distributional modelling</td>
<td>Harbour high levels of genetic diversity that help prevent extinction and may facilitate evolution</td>
</tr>
<tr>
<td>Confirmation of niche conservation</td>
<td>Phylogeny</td>
<td>Organelle and nuclear DNA, distribution of species and associated climatic variables</td>
<td>Regional/Continental</td>
<td>Distributional modelling</td>
<td>An important assumption to test when modelling species distribution</td>
</tr>
<tr>
<td>Which parts of the landscape matrix facilitate or prevent gene flow</td>
<td>Landscape genetics</td>
<td>Microsatellites or AFLPs, landscape and climatic data</td>
<td>Landscape</td>
<td>Population demographic modelling</td>
<td>Gene flow is essential to maintaining strong meta-population structure</td>
</tr>
<tr>
<td>Habitat characteristics associated with source and sink populations</td>
<td>Source-sink framework</td>
<td>Microsatellites or AFLPs, landscape and climatic data</td>
<td>Landscape/Local</td>
<td>Population demographic modelling</td>
<td>Identify what habitat characteristics are required for self-sustaining populations</td>
</tr>
<tr>
<td>Location of areas with heightened adaptive potential</td>
<td>Phylogeny/Landscape genetics</td>
<td>Organelle and nuclear DNA, microsatellites and AFLPs</td>
<td>Regional/Continental</td>
<td>Population demographic modelling</td>
<td>Promote in situ adaptation to changing conditions</td>
</tr>
<tr>
<td>Location of adaptive loci in a species meta-population</td>
<td>Landscape genetics</td>
<td>Microsatellites, AFLPs or candidate gene markers</td>
<td>Landscape</td>
<td>Population demographic modelling</td>
<td>Identify adaptive potential of different populations within a given species</td>
</tr>
</tbody>
</table>
Figure 1 Modelled species distributions under past and future climates. Publications (2008–July 2009 only) were sourced within the Zoological Record’s database using the topic search ‘climate change AND model*’ and ‘range OR distribution’. Future distributions are divided into those generated using bioclimatic models (‘Modelled’) and those inferred on the basis of empirical studies and/or expert knowledge (‘Inferred’). Past distributions were all bioclimatically modelled and are divided on the basis of temporal scale; those considering distributions <500 years ago (‘Recent’) and those considering distributions >500 years ago (but generally investigating the last glacial maximum ‘Ancient’). Black bars indicate the proportion of studies (number of studies indicated within the bars) that did not utilize information derived from molecular marker studies and white bars those that did. For a full listing of references used and their classification under this system, see Appendix S1 in Supporting Information.

and the testing of temporal niche conservatism. For landscape genetic approaches, we consider the quantification of landscape permeability and source/sink dynamics of meta-populations and the identification of adaptive variation in the landscape. A summary of parameters that are derivable from such studies for modelling and conservation applications is provided in Table 1.

LESSONS FROM THE PAST: CONSULTING THE TEMPORAL RECORD TO PREDICT THE FUTURE

Phylogeography seeks to interpret patterns of inter and intraspecific genetic diversity in a combined phylogeographic and geographical framework, to understand historic population demography and structure (Avise et al., 1987). Phylogeographic analyses enable the identification of historic barriers to dispersal and refugia (locations that maintain environmental suitability for species during environmental change; Avise et al., 1987; Moritz et al., 1987; Zink & Barrowclough, 2008; Joseph & Omland, 2009). Such analyses generally focus on organelar variation but more recently nuclear-encoded variation has been used to examine timings of coalescence, gene flow and changes in population size across multiple loci (Edwards & Beerli, 2000; Zink & Barrowclough, 2008; Table 1).

Phylogeography has most often been applied to explore the impact of Quaternary climate oscillations on the distribution and resilience of species (Martinez-Meyer et al., 2004; Carstens & Richards, 2007; Bhagwat & Willis, 2008; Kearns et al., 2009). Of particular interest is the impact of recent glacial cycles, where global ecosystems experienced a substantial reduction in temperature and widespread aridity, resulting in desertification in some areas (White, 2006) and the formation of land ice in others (Bhagwat & Willis, 2008; Stewart et al., 2010). Such major historical ecosystem upheavals have had a lasting impact on the genetic variation resident within species, and phylogeographic methods can be used to identify signatures of historical genetic discontinuities or location of species refugia within contemporary populations.

Identifying barriers from a long-term, evolutionary standpoint

The Eyrean barrier in southern Australia is an example of important Quaternary aridity barrier, which in some cases still acts as a barrier to migration today. Such barriers are commonly believed to be implicit in biogeographic patterning (Ford, 1974, 1987), although in some cases molecular evidence is wanting (Joseph & Omland, 2009). By identifying barriers such as those in the landscape, two objectives are possible. First, by identifying long-term barriers to migration, it is possible to more realistically model species response to contemporary climate change. Suitable climatic space will be irrelevant if barriers to migration prevent individuals from reaching such areas. Secondly, by identifying suture zones across former barriers (areas of hybridization between formally separated populations), it is possible to identify likely sites of future evolutionary potential. This application was considered by Vandergraaff et al. (2008), who observed ‘divergence hotspots’ for 21 southern Californian taxa were most often associated with suture zones.

Taking shelter from the storm: locating refugia

Refugia are locations where species may persist through periods of stress, including climatic extremes (Mackey et al., 2002). Some refugia are important over long time scales and may be identified through phylogeographic studies. Long-term refugia may be defined as those that species populate for at least an entire glacial-interglacial cycle (Stewart & Dales, 2008; Stewart et al., 2010) and are generally locations, which harbour high levels of algal diversity.

One of the first spatially explicit approaches to identifying refugia was used by Hugall et al. (2002), who combined molecular phylogeography and palaeoclimatological modelling to locate Pleistocene refugia by projecting a species’ environmental envelope onto palaeoclimatic surfaces. In this study, palaeoclimatological modelling predictions of refugial location and temporal change in the distribution of suitable habitat were found to be consistent with phylogeographic analyses for the land snail, *Gnouvophis* bentendenensis.

Statistical phylogeography has recently been developed to facilitate the identification of causal processes in biogeography.
and offers a robust method to identify both barriers and refugia. The method involves examination of competing phylogeographic hypotheses of a species’ history generated from a priori models of population structure and statistically assessing the stochastic expectations of each against patterns of observed genetic variation (Knowles & MacIsaac, 1992; Knowles, 2004). Richards et al. (2007) used this method to assess whether contemporary, isolated ‘sky island’ populations of the flightless montane grasshopper (Melanoplus marshalli) were colonized from proximate refugia as opposed to a single ancestral population (the null hypothesis) (Knowles et al., 2007). When compared to model outputs of the two hypotheses, genetic data most closely fitted a multiple refugial scenario.

**Highlighting community patterns**

Testing alternative refugial scenarios and assessing what processes have shaped community structure under historical climates can be explored through comparative phylogeographic analysis of multiple species (Bermingham & Moritz, 1998). Comparative phylogeography is a particularly valuable approach because it enables the identification of long-term barriers and refugia common to groups of species and is consequently highly relevant to conservation planning. Carstens & Richards (2007) considered alternative refugial scenarios for four contemporary co-distributed species in the Pacific Northwest montane forest ecosystem of North America. Whilst the contemporary distribution of all species is similar, paleodistributions were markedly different and were then used for generating phylogeographic hypotheses. A model of population history was defined for each species, considering the order and timing of population divergence. Results indicated that the amphibian lineages (Asclepius lycaeides/Asclepius triseriata and Phlebolepsis idahoensis/Phlebolepsis owyheensis) had responded as a cohort and have been restricted to two refugia, within the Cascades and northern Rocky Mountains. However, the water vole (Microtus richardsoni) and willow, (Salix melanopis), which exhibit similar genetic patterns, had very different refugial patterns; the vole restricted to the Cascades, and the willow to the northern Rocky Mountains (Carstens & Richards, 2007).

**The ability to test niche conservatism, a fundamental assumption of climate-niche modelling**

The output of bioclimatic models has been called into question by some because of concerns over the validity of underlying assumptions (e.g. Araujo et al., 2005a,b). One fundamental assumption is that a species’ niche remains constant over time. By characterizing the ecological niche of contemporary populations using known distribution points and correlated ecological data, there is an assumption that the species in question will inhabit the same ‘ecological space’ for the projected time period. Hence, an important step in assessing the validity of bioclimatic modelling approaches should be to gain an estimate of the accuracy of predictions of spatial distribution under a changed climatic scenario (Pearson & Dawson, 2003). Evaluation can be achieved if long-term temporal datasets exist (Araujo et al., 2005a,b), or by looking back in time using the fossil record.

In a study of 23 extant North American mammal species Martinez-Meyer et al. (2004) employed hindcasting approaches, verified by a fossil record, to test the accuracy of ecological niche conservatism. Ecological niche envelopes were developed for all species using the Genetic Algorithm for Rule Set Prediction (GARP). Model predictions (based on contemporary occurrences) were tested by projecting the modelled ecological niche onto Pleistocene paleoclimates, and statistically assessing the location of fossil remains in relation to the niche predictions (Martinez-Meyer et al., 2004). Likewise, an ecological niche based on species distribution from the Pleistocene (using fossil data) was used to project present-day distributions and compared to contemporary occurrence points. Of the 23 species considered, predictions for nine species corresponded significantly in both temporal directions, a further three species were significant using a Pleistocene-derived niche to model contemporary distributions, and five species significant when hindcasting. Whilst this is strong evidence for temporal niche conservatism in North American mammals, the study also demonstrated the necessity of testing for niche conservatism, since five species demonstrated no predictivity of modelled niche in either direction.

The use of fossils to test ecological niche conservatism is a powerful approach; unfortunately, the fossil record may be rare or non-existent for some species groups or locations. In such cases, niche conservatism can be tested using the distribution of molecular variation in contemporary populations as an indicator of historical range. Peterson & Nyari (2008) used GARP to test for ecological niche conservatism in the thrush-like mockingbird (Sicalis flaveola) complex in the neotropics. The modelled niche of seven genetic clusters (or phylogeographic groups) identified within the species complex was initially tested for predictivity both across space and by lineage membership. Once predictivity within contemporary climatic conditions was demonstrated, the ‘best-subsets models’ were projected onto paleoclimate characteristic of the last glacial maximum (LGM), to test the ability of climatic refugia to explain the distribution of molecular phylogroups. Using this approach, climatic refugia were able to predict the geographic structure of phylogroups better than by chance alone, confirming ecological niche conservatism for this species complex.

The integration of a statistical framework into a phylogeographic approach allows a rigorous assessment of alternative distributional scenarios during different time periods and offers the ability to identify the biogeographical processes operating both at the level of individual species and comparatively across a given community. Understanding refugial patterns and how species adapted and evolved in response to previous climatic extremes provides an important insight for future changes in climate.
MY, HOW THINGS HAVE CHANGED: HUMAN INFLUENCE ON THE LANDSCAPE AND BIOTA

Expanding urban centres and agricultural practices are decreasing the quality, connectivity and amount of native habitat available for many species (Hannah et al., 2002; Opdam et al., 2003; Opdam & Wascher, 2004; Foley et al., 2005; Vos et al., 2008). Recent landscape ecological approaches (Hanski, 2004) no longer recognize elements of the landscape outside native habitat patches as uniform, but instead as a heterogeneous matrix in which some elements can enhance connectivity and gene flow between increasingly fragmented populations (Ricketts, 2001). Empirical studies (e.g. Brooker & Brooker, 2002) have demonstrated that it is the landscape matrix that most impacts dispersal and persistence of spatially structured meta-populations. Consequently, the whole landscape may be considered a ‘functional template for biodiversity’ (i.e. its environment), and it is at the spatial scale of the landscape that anthropogenic land-use changes occur and dominate (Opdam et al., 2003).

The synergistic effect of habitat fragmentation and climate change puts increasing pressure on species persistence, but maintenance of strong meta-population structure, via gene flow, will enable species to recolonize following disturbance events (Opdam & Wascher, 2004). The value of landscape connectivity in enabling species to track changes to their environmental envelope (Hannah, 2008) is now being increasingly recognized (Bradshaw & Holzapfel, 2006). Yet, modelling studies assessing a species distribution under climate change often assume that the habitat is homogeneous (Opdam & Wascher, 2004). Furthermore, species characteristics that dictate its ability to respond to changes in habitat distribution, are rarely considered, and include; mobility, dispersal characteristics and source/sink dynamics within a meta-population structure.

A new approach to understanding the relative effect of mosaic attributes on meta-population dynamics comes from the integration of landscape ecology and population genetics, landscape genetics (Manel et al., 2003). Landscape genetics seeks to understand how microevolutionary processes, such as gene flow, genetic drift and selection operate within the landscape mosaic to structure populations, without the a priori identification of populations (Manel et al., 2003; Storfer et al., 2007). In particular, landscape genetics seeks to understand how landscape features have shaped genetic variation, but focuses on contemporary events and at a smaller geographic scale than phylogeography (Joseph & Ormand, 2009). A range of molecular marker types can be used for such studies (e.g. Sannaacks & Taylor, 2008; Lowe et al., 2004; Table 1).

Whilst comprehensive research agendas (Storfer et al., 2007) and potential future directions (Holegerger & Wagner, 2008; Balkenhol et al., 2009) have been published for landscape genetics, the impressive number of studies assessing genetic connectivity using this framework (Balkenhol et al., 2009) is rarely used to inform species modelling approaches. We outline here the potential utility of these approaches for informing species demographic planning decisions under future climate change scenarios.

Identifying aspects of the landscape matrix that facilitate and disrupt gene flow

Assessing the permeability of the matrix between habitat remnants is probably one of the most common applications within the field of landscape genetics. Amongst a vast array of options (Storfer et al., 2007), the most popular approach has been to use least-cost path (LCP) modelling. LCPs differ from Euclidean geographic distances by calculating effective distances between habitat patches based on the species-specific cost of moving through particular landscape features, as well as considering behavioural characteristics of the species in question (Adriaensen et al., 2005). In a study of the American marten (Martes americana), least-cost distances, based on individuals avoiding known dispersal barriers such as logging sites and undeveloped forest stands, better explained pairwise genetic distances than did Euclidean geographic distances (Broquet et al., 2006). Likewise, studies on the European roe deer found that pairwise population genetic distances were best explained by least-cost distance (Goulon et al., 2004). Furthermore, it was shown that two populations had likely diverged because of several high resistance barriers (e.g. roads) that reduced roe deer movements (and hence gene flow (Goulon et al., 2006)).

Barriers to connectivity and gene flow may not always be as obvious as roads or areas of deforestation. Environmental gradients, such as temperature gradients (Dionne et al., 2008) or snow melt gradients (Hirao & Kudo, 2004), can restrict gene flow similar to more obvious barriers but are of particular interest when likely to alter under climate change. Information generated by LCP on likely barriers and dispersal routes can also be used to inform the design of corridors enabling short and long distance movement (Ippol et al., 2007).

Novel methods to assess connectivity

LCP is somewhat limited in its ability to accurately model gene flow in real populations (McRae & Beier, 2007; Murphy et al., 2008), rather gene flow is likely to occur via numerous direct pathways through the landscape and using indirect stepping stone movements over more than one generation (Slatkin, 1993; McRae & Beier, 2007). Therefore, understanding dispersal pathways is better served by methods that consider multiple pathways, such as isolation by resistance (IBR). Distance metrics based in electrical circuit theory have provided the basis for IBR, based on analogous characteristics between conductivity and gene flow (McRae, 2006). Increasing the number and width of conductive pathways increase conductivity much in the same way that gene flow might increase should the same principles be applied to landscape connectivity (McRae, 2006; McRae & Beier, 2007). IBR represents an improvement on LCP methods because of its strong theoretical foundation described by the connection...
between the timing of gene coalescence in a given meta-
population and measures of effective resistance in a landscape
matrix (McRae, 2006). The effectiveness of this approach was
assessed for central American populations of the big-leaf
mahogany (Swietenia macrophylla) and North American
populations of the willowleaf (Gala gula) (McRae & Beier,
2007). IFR analysis outperformed both LCP and isolation by
distance approaches in the ability to explain gene flow within
each species meta-population because of a capacity to consider
range shape, as well as multiple pathways and individual
widths simultaneously.

The potential of landscape genetic approach could also be
greatly enhanced with the development of analyses that can
investigate the effect of multiple environmental variables and
interactions within a single population genetic model (Storfer
et al., 2007). To date, analyses have most often relied on simple
Mantel tests to integrate landscape information with popula-
tion genetics (Storfer et al., 2007; Pavlacky et al., 2009), despite
the likely violation of the stringent assumptions of the test
(Bossart & Prowell, 1998), and non-independence of genetic
similarity measures between populations (Yang, 2004). In an
attempt to develop a more robust landscape genetic frame-
work, Pavlacky et al. (2009) employed a linear mixed model
(Yang, 2004), to estimate appropriate sampling variance and
distinguish between contemporary and historic landscape
factors influencing genetic connectivity of the logger (Oryctolagus
tenrecinchi). This approach demonstrated that whilst spatial heterogeneity for rainforest and sclerophyll
woodland elements enhanced dispersal historically, contem-
porary migration rates were strongly disrupted by anthropo-
genic deforestation (Pavlacky et al., 2009). The linear mixed
model provides a mechanistic measurement of logger dispersal through different landscape features, allowing an
improvement in precision compared with LCP, e.g. (Courell,
2004; Broquet et al., 2006; Coulson et al., 2006) that rely on
hypothetical migration routes (Pavlacky et al., 2009).

Characterizing meta-population source–sink dynamics

Within a spatially structured population, migration through
the landscape matrix facilitates a balance of local births, deaths,
immigration and emigration that influence population density
at a given point in time (Stanis, 2004). Such populations can
be characterized within a source–sink framework (Pulliam,
1988), where populations are defined on the basis of net
emigration (sources) or net immigration (sinks). This frame-
work allows the demographic and habitat features associated
with robust or alternatively, unstable populations, to be
identified. This approach was employed to understand the
impact of old-growth forest harvesting on the population
viability of a threatened seabird, the Marbled Murrelet
(Brachyrhania marcola) (Peery et al., 2008). The smallest
Murrelet population is located in central California, United
States of America, and is considered a sink because of its
isolation from other populations, low birth rate and immi-
gation estimates from mark-recapture studies (Peery et al.,
2006). To test this hypothesis, the number of parent–offspring
dyads expected under both a closed (self-sustaining) and sink
population was modelled using variables of expected demo-
graphic characteristics. Demographic models were compared
to estimates derived from a random sample of individuals from
the central Californian population, using the frequency of
parent–offspring dyads using multifaceted genetic profiles. The
estimated number of parent–offspring dyads was best
explained by the modelled sink populations experiencing
4–6% immigration annually, and hence the null hypothesis
of a self-sustaining population could be rejected. Interestingly,
an earlier mark-recapture study reported immigration rates of
16% (Peery et al., 2006), suggesting that in some situations
migrants are selected against, or do not permanently relocate
to the central Californian population (Peery et al., 2006).

Investigating a meta-population under a source–sink frame-
work can also extend to characterizing the effect of the
intervening matrix on dispersal between populations, as well as
consideration of different spatial scales. Historical population
demography and contemporary dispersal and restructuring were
examined using molecular marker methods on the common
European toad, Bufo bufo (Martinez-Solano & Gonzalez,
2008). Separate phylogeographic clades were identified in
Morocco and the Iberian Peninsula, but neither exhibited
within region geographically structuring, indicating gene flow
throughout the two regions. Analysis of heterozygosity values
indicated that whilst most populations are self-sustaining,
some exhibited low levels of heterozygote excess, indicative of
‘sinks’, and assignment tests could be used to identify the
probable sources. The influence of landscape variables on
dispersal permeability was assessed within the central Spanish
populations. Results indicated that gene flow both within and
between ecosystems was similar, demonstrating that riverine
habitats in this region do not play an important role in
facilitating dispersal. Conversely, higher altitude populations
exhibited increased levels of genetic differentiation indicating
that altitude might impede dispersal in this species.

Beyond neutral gene flow: identifying the potential
evolution and adaptation

Whilst many species may undergo changes in their distribu-
tional range in response to environmental change, others will
adapt to changing conditions. In particular, steep environ-
mental gradients are often associated with adaptive variation,
reflected in high levels of genetic divergence across the gradient
(Mortiz, 2002; Vandergast et al., 2008), and are increasingly
recognized as relevant to preserving evolutionary potential. For
example, in the Subtropical Thicket Biome of South Africa
(Rouget et al., 2006), regional conservation corridors have
been designed around major rivers to capture environmental
gradients. Amongst the biodiversity features considered were
biome interfaces, as well as topographical and macroclimatic
gradients. Klein et al. (2009) likewise considered both ecolog-
ical and evolutionary refugia in their recent conservation plan
for Australia. They sought to identify 'evolutionary refugia';

Diversity and Distributions 16, 343–355, © 2010 Blackwell Publishing Ltd
places in the environment that facilitated species persistence and radiation during periods of high climatic and/or environmental stress (Morton et al., 1995).

When considering individual species, capturing recent, local adaptation has been greatly enhanced by the recent increased availability and use of adaptive gene markers (Gebermedhin et al., 2009). Bonin et al. (2007) developed a population adaptive index (PAI) that identifies outlier loci, which are candidates for selective action and exhibit increased differentiation compared to neutral population parameters such as gene flow (Nei, 2005; Store, 2005). Bonin et al. (2007) applied this concept to the common frog (Rana temporaria) and the Austrian dragonhead (Dracocephalum austriacum). For both species, measures of neutral and adaptive variation did not coincide, indicating that protecting neutral genetic diversity does not necessarily mean that current adaptive potential is also preserved. However, it is worth noting that adaptive loci identified by methods such as PAI may not necessarily represent adaptive potential in the future under novel threats (Bonin et al., 2007; Gebermedhin et al., 2009). It is likely that adaptive loci will complement neutral genetic diversity that currently represents our best measurable way of identifying evolutionary potential at the intra-specific level. However, the techniques to screen such adaptive variation are still developing. At present, the incorporation of adaptive gene information into modelling studies may allow a useful understanding of the distribution of adaptive variation associated with a single strong selective force. However, to progress modelling that combines a broader range of active and latent adaptation will require much more work both from the genomics and modelling fields.

CONCLUSIONS

Molecular marker methods offer a unique chance to step back in time to assess historical rangewide and demographic changes and understand links with past environmental change. By incorporating such information into species distribution modelling approaches, we should be able to improve our future predictions of species distribution and demographic trajectories.

Of particular relevance to species distribution modelling approaches, molecular marker studies can identify biogeographic barriers that may still limit species movement, and hence impact on future responses to climate change. Alternatively, former barriers that are now hybrid zones between previously isolated populations may harbour important evolutionary potential and warrant protection. Historical refugia can likewise be identified, the location of which can be used to independently verify hindcasting species distribution modelling. Statistical phyleogeography provides a rigorous framework for testing alternative hypotheses of species and community response to biogeographical processes associated with historical climatic extremes. Furthermore, by examining the concept of niche conservatism, it is possible to test a fundamental assumption of bioclimatic models.

In addition to advancing understanding of historical range change dynamics, molecular marker approaches can also further understanding of contemporary population demography and its relationship to recent land-use changes. Human activities, through habitat fragmentation, introduction of invasive and climate forcing are altering the composition and distribution of natural ecosystems. It is therefore imperative that species modelling approaches consider the influence of the contemporary landscape matrix on evolutionary processes and consequent meta-population structure. Molecular approaches such as landscape genetics, which can identify contemporary gene flow barriers and source–sink dynamics, are well placed to robustly inform modelled species distributions under future climate change.

ACKNOWLEDGEMENTS

We thank Leo Joseph and Anita Smyth at CSIRO Sustainable Ecosystems and Climate Adaptation Flagship, Peter Cale and Jaco Le Roux for comments on the manuscript, and J.S. acknowledges the support of a CSIRO Climate Change Flagship postgraduate top up grant for this work.

REFERENCES

Bilbagwi, S.A. & Willis, E.J. (2008) Species persistence in northernly glacial refugia of Europe: a matter of chance or


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article: Appendix S1 References screened for data used in Fig. 1 and their classification.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.

**BIOSKETCH**

Jolene Scoble is currently completing her PhD in genetic analysis of the southern scrub-robin to elucidate metapopulation structure, and understand historical and contemporary dispersal across ecotones between intact and residual mallee vegetation in South Australia. Andrew Lowe leads a research group that apply molecular markers, landscape analysis and genomic assessments of adaptive genes, to demonstrate gene flow and selection pressure changes across a range of landscapes; contemporary, historical, fragmented and exploited.

Author contributions: A.J.L. and J.S. conceived the ideas; J.S. searched and collated the literature; and J.S. and A.J.L. shared the writing.

Editor: David Richardson
Chapter 3:

Isolation via 454 sequencing, and characterisation of microsatellites for Drymodes brunneopygia, southern scrub-robin (Aves: Petroicidae): a species at risk due to substantial habitat loss and climate change

Jolene A. Scoble$^{1,2}$, Andrew J. Lowe$^{1,3}$ and Michael G. Gardner$^{1,4,*}$

$^1$ Australian Centre for Evolutionary Biology and Biodiversity, School of Earth and Environmental Science University of Adelaide, North Terrace, SA 5005, Australia.

$^2$ CSIRO, Climate Adaptation Flagship, GPO Box 1700, Canberra, ACT 2601, Australia.

$^3$ State Herbarium of South Australia, Science Resources Centre, Department of Environment and Natural Resources, Adelaide, SA 5005, Australia.

$^4$ School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide 5001 South Australia, Australia and Australian Centre for Evolutionary Biology and Biodiversity.

$^*$Corresponding author. Email: michael.gardner@flinders.edu.au, Phone: +61 8 8201 2315
STATEMENT OF AUTHORSHIP

Isolation via 454 sequencing, and characterisation of microsatellites for Drymodes brunneopygia, southern scrub-robin (Aves: Petroicidae): a species at risk due to substantial habitat loss and climate change

This chapter has been accepted for publication in Conservation Genetics Resources.

Jolene Scoble
Completed all laboratory work and data analysis, and prepared manuscript as principle author.

Signed:
Date: 27/01/2012

Andrew John Lowe
Provided guidance on laboratory work and data analysis, and commented on manuscript.

Signed:
Date: 30/01/2012

Michael George Gardner
Provided guidance on, and assisted with laboratory work and data analysis, and helped write manuscript.

Signed:
Date: 24/01/2012
Permission to reprint

This is a License Agreement between Jolene Scoble (“You”) and Springer (“Springer”) provided by Copyright Clearance Center (“CCC”). The license consists of your order details, the terms and conditions provided by Springer, and the payment terms and conditions.

All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

License Number: 2839110630145
License date: Jan 30, 2012
Licensed content publisher: Springer
Licensed content publication: Conservation Genetics Resources
Licensed content title: Isolation via 454 sequencing, and characterisation of microsatellites for Drymodes brunneopygia, southern scrub-robin (Aves: Petroicidae): a species at risk due to substantial habitat loss and climate change
Licensed content author: Jolene A. Scoble
Licensed content date: Jan 1, 2011
Type of Use: Thesis/Dissertation
Portion: Full text
Number of copies: 1
Author of this Springer article: Yes and you are a contributor of the new work
Order reference number: 31012012
Title of your thesis / dissertation: No place to go and nowhere to be? Characterising demography of the southern scrub-robin (Drymodes brunneopygia) using molecular and modelling tools for conservation
Expected completion date: Feb 2012
Estimated size (pages): 210
Total: 0.00 USD

Terms and Conditions

If you would like to pay for this license now, please remit this license along with your payment made payable to "COPYRIGHT CLEARANCE CENTER" otherwise you will be invoiced within 48 hours of the license date. Payment should be in the form of a check or money order referencing your account number and this invoice number RLINK5607059446.
Once you receive your invoice for this order, you may pay your invoice by credit card. Please follow instructions provided at that time.

Make Payment To:
Copyright Clearance Center
Dept 001
P.O. Box 843006
Boston, MA 02284-3006

For suggestions or comments regarding this order, contact RightsLink Customer Support: customercare@copyright.com or +1-877-622-5543 (toll free in the US) or +1-978-646-2277.
Gratis licenses (referencing $0 in the Total field) are free. Please retain this printable license for your reference. No payment is required.

**NOTE:**
This publication is included on pages 42-44 in the print copy of the thesis held in the University of Adelaide Library.

It is also available online to authorised users at:

http://dx.doi.org/10.1007/s12686-011-9540-2
Chapter 4:

Between a rock and a hard place – molecular implications of habitat fragmentation and protection for the Australian southern scrub-robin (*Drymodes brunneopygia*)

Jolene Scoble¹ ², Peter Cale³, Michael George Gardner¹ ⁴, Anita Smyth⁵ and Andrew John Lowe¹ ⁵ ⁶*

¹ Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, North Terrace, Adelaide, SA 5005, Australia.

² CSIRO, Climate Adaptation Flagship, GPO Box 1700, Canberra, ACT 2601, Australia.

³ Australian Landscape Trust, Calperum Station, PO Box 955, Renmark SA 5341

⁴ School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide 5001, Australia

⁵ Eco-informatics Facility, Terrestrial Ecosystem Research Network, University of Adelaide, North Terrace, SA 5005, Australia.

⁶ State Herbarium of South Australia, Science Resources Centre, Department of Environment and Natural Resources, Adelaide, SA 5005, Australia.

*Corresponding author: andrew.lowe@adelaide.edu.au

Running head: molecular implications of habitat fragmentation for the southern scrub-robin

Article type: Empirical research
STATEMENT OF AUTHORSHIP

Between a rock and a hard place – molecular implications of habitat fragmentation and protection for the Australian southern scrub-robin (*Drymodes brunneopygia*).

This chapter has been prepared as a submission for publication.

**Jolene Scoble**
Sought and won funding, designed and executed field sampling, completed all laboratory work and data analysis, and prepared manuscript as principle author.

Signed:
Date: 27/01/2012

**Peter Cale**
Assisted with design and execution of field sampling.

Signed:
Date: 21/01/2012

**Michael George Gardner**
Provided guidance on, and assisted with laboratory work and data analysis, and commented on manuscript.

Signed:
Date: 24/01/2012

**Anita Smyth**
Assisted with design and execution of field sampling.

Signed:
Date: 19/01/2012
Andrew John Lowe
Assisted with design of field sampling, provided guidance on laboratory work and data analysis, and commented on manuscript.

Signed:
Date: 30/01/2012
Abstract

Worldwide, agricultural practices fragment native habitat. They alter evolutionary processes of resident species and so can result in increased genetic diversity between populations and the erosion of genetic diversity within them. Within Australia, species are pre-adapted to climatic extremes; however the synergy of anthropogenically forced climate change and habitat clearance has serious implications for Australian species. At particular risk are species with limited dispersal capabilities and specific habitat requirements.

We characterise patterns of genetic diversity for one such species, the southern scrub-robin (*Drymodes brunneopygia*) within agricultural and relatively intact landscapes in both Western Australia and South Australia. We assess the suitability of current protected areas for conserving this species. We find that large areas of contiguous native vegetation are most often conserved toward the climatically extreme, northern distribution of the southern scrub-robin. Conversely, we find that genetic diversity and larger effective population size are concentrated in southern regions, which are dominated by agriculture. These patterns were particularly evident in South Australia. Expected heterozygosity ($R^2 = 0.6702$), allelic richness ($R^2 = 0.6748$) and private alleles ($R^2 = 0.1381$) were all positively correlated with latitude. Effective population size was positively correlated with both latitude ($R^2 = 0.1221$) and reporting rate ($R^2 = 0.1643$), while negatively correlated with inbreeding ($R^2 = 0.0551$). Conservation efforts should be oriented toward protecting populations of the southern scrub-robin in habitat fragments embedded in the agricultural matrix that continue to maintain high levels of genetic diversity and are likely to remain climatically appropriate, in preference to areas protected simply due to agricultural unsuitability.
Introduction

Worldwide, the loss and fragmentation of habitat are undoubtedly among the greatest ongoing threats to biodiversity. Anthropogenic development has resulted in immense loss of, and modification to natural habitats, occurring most intensively in areas where fertile soils and climates appropriate for agriculture are located. Consequently, a diverse range of species found within such regions frequently suffer from fragmented distributions that alter evolutionary processes and result in increased population structure and the erosion of genetic diversity (Stow et al. 2001, Schmuki et al. 2006, Walker et al. 2008, Pavlacky et al. 2009). Despite increasing community concerns about the state of the environment, clearing of native ecosystems has been ongoing in the 21st century (e.g. Beeton 2006). Augmenting the effect of habitat clearing and alteration, climate change is predicted to have serious implications for the future of biodiversity. Species have evolved with a climate that has substantially oscillated over time (Byrne 2008b, Mackey et al. 2008) and many species exhibit adaptations to climatic change (Soule et al. 2004). What makes anthropogenic climate change a major threat is that its impact will occur in ecosystems already suffering fragmentation and other perturbations associated with human activities (Mackey et al. 2008). Many species rely heavily on protected area networks as a buffer against habitat loss and other human based threats. Their ability to protect species’ genetic diversity and facilitate adaptive potential to novel threats such as climate change remains largely unexamined.

Protected areas undoubtedly have an important role to play as species face enormous challenges associated with anthropogenic habitat clearing and climate change. However the current reserve system requires a substantial overhaul if it is to meet this challenge. Historically, protection was frequently afforded to regions that were unsuitable for agriculture or urbanisation, rather than on the basis of inherent biological value. Many ecosystems and resident species are thus underrepresented in the reserve system (Fuller et al. 2010). Furthermore, reserves are often at the edge of productive agricultural land, coinciding with the boundary between different climate and/or vegetation zones which frequently represent the fringe of a species’ distribution. This has important ramifications for safeguarding genetic diversity, which is predicted to be highest at the centre of a species’
distribution. The abundant centre model suggests that conditions are optimal at the centre of a given species’ distribution, leading to higher effective population sizes and levels of gene flow (Vucetich and Waite 2003, Eckert et al. 2008). Extending this idea to consider the genetic implications of the abundant centre model, effective population size and the rate of gene flow ought to be highest in the central area of species’ distribution, decreasing with proximity to range margins (Vucetich and Waite 2003, Eckert et al. 2008). Conservation science is increasingly recognising the importance of safeguarding species’ distributions and the evolutionary processes maintaining species’ abundances and hence adaptive capacity (Klein et al. 2009, Sgro et al. 2011). Uptake of this has, to date, been slow for conservation planning and on-ground adaptation (Dunlop 2008).

Here we assess the effectiveness of current protected areas for the conservation of the southern scrub-robin (*Drymodes brunneopygia*), a ground dwelling Australo-Papuan robin (Passeriformes: Petroicidae) distributed throughout the semi-arid mallee region of southern Australia (Higgins and Peter 2002). The effect of climate change on Australian species in arid and semi-arid zones, which constitute some 75% of the continent, has been largely overlooked to date (Hobbs et al. 2008, Hughes 2011). This is despite indications that climate change is likely to have some of the most serious implications for arid ecosystems. Preliminary studies in the northern hemisphere suggest that lowland desert-dwelling bird species may be at greater threat than montane species from contemporary climate change (Peterson et al. 2002, Peterson 2003). Furthermore, habitat quality and connectivity are already more likely to be diminished in lowland habitats, as extensive human disturbance is less prevalent in montane environments due to topographic restrictions (Hannah et al. 2002).

The southern Australian distribution of the southern scrub-robin lies within moderate rainfall areas favourable for agriculture. This has resulted in high levels of habitat loss and fragmentation in many regions and produced a mosaic of remnant habitat patches of varying size and geographical isolation. Protection of habitat for the southern scrub-robin and other species inhabiting the mallee region of Australia has largely occurred in the northern fringes of this region, where climate and soil types are unsuitable for broad-acre cropping. This habitat configuration makes the southern scrub-robin an
ideal model species for investigating both the efficacy of the protected area network across southern Australia for protecting genetic diversity and gene flow in this species, as well as its ability to buffer against the effects of climate change.

Because of the southern scrub-robins’ susceptibility to habitat modification (Ford et al. 2001), and the nature of ongoing climate change, characterisation of its genetic connectivity and diversity for conservation is essential. The aim of this study was to characterise genetic diversity, population structure and recent migration for remnant (located in reserves embedded in agricultural areas) and natural (located in reserves not isolated by agriculture) populations across the Wheatbelt region of Western Australia, and the Flinders Ranges National Park, and Murray-Darling Rivers Basin regions of South Australia. We investigate two competing hypotheses. Firstly, we hypothesise that effective population size and the rate of gene flow will be highest in the central area of species’ distribution, decreasing with proximity to range margins (using latitude as a proxy for distance from the centre of distribution). However, we also investigate whether agricultural habitat loss and isolation of populations close to the centre of the southern scrub-robins’ distribution has eroded genetic diversity. We hypothesise that remnant populations will have diminished genetic diversity, higher levels of inbreeding, and decreased levels of gene flow compared with their natural counterparts.

Materials and methods

Study species and sampling regions

The southern scrub-robin is a ground dwelling species’ whose life history is dependent on the health of ground habitat. Individuals search for food (invertebrates and seeds) within the litter layer, nest on or close to the ground, and are heavily reliant on low shrubs for protection from mammalian and avian predators (Schodde 1981, Higgins and Peter 2002). Unlike many other birds adapted to arid conditions, the scrub-robin lays only a single egg and clutch size does not increase when conditions are favourable; it has a low annual fledgling production rate (Brooker 2001). The southern-scrub
robin is known to avoid using and nesting near anthropogenic habitat edges, which may increase levels of predation (Luck et al. 1999). Additionally, the species decreases in abundance where grazing has diminished vegetative ground cover (Cale and Mladovan 2007). It is unsurprising, then, that sedentary ground dwelling species such as the southern scrub-robin are considered disproportionately threatened by human activity compared with birds having different life histories (Reid and Fleming 1992, Ford et al. 2001). While the scrub-robin is listed as of *least concern* (The Action Plan for Australian Birds 2000 (Garnett and Crowley 2000)) and is not listed as threatened under the Environment Protection and Biodiversity Conservation Act 1999, populations are disappearing from fragments and the species has a decreasing area of occupancy (Garnett and Crowley 2000).

Using the method outlined by Pavlacky et al. (2009), we assume the southern scrub-robin has a generation time, G, of $G = \alpha + s/(1 - s)$, where $\alpha =$ age at first reproductive event, and $s =$ survival rate (Lande et al. 2006). Given typical passerine characteristics of first reproduction occurring at one year old, and an adult survival rate of 0.75 (Yomtov et al. 1992), we assume the southern scrub-robin has a generation time of four years and that some 25 generations have passed since agricultural clearing began in our study regions during the early 1900’s.

Between 11 and 22 (mean = 17) southern scrub-robins were sampled from each of 17 locations during 2009 and 2010 which were on average 2km² (Table 4.1, Figure 4.1). In Western Australia, five locations were sampled throughout the Wheatbelt region (also includes Francois Peron NP, which lies just north of the Wheatbelt in the Shark Bay World Heritage Area). The Western Australian Wheatbelt (longitude: 118.000, latitude: -32.000) covers some 14 million hectares, and is broadly defined as receiving between 280 and 600mm rainfall annually (Prober and Smith 2009). It was predominantly cleared in the 1900s. Around 36% was cleared by 1920, and by 1984 clearing had peaked at 93% (Prober and Smith 2009). In South Australia, five populations were sampled within each of the south (Murray Mallee) and north (Riverland Biosphere Reserve) Murray-Darling Rivers Basin region and, and two from the Flinders Ranges region. The Murray Mallee (140.200, -34.800) is the grain-growing and sheep-farming area of South Australia bounded to the north and west by the
The Murray River, to the east by the Victorian border. Two of our southern Murray-Darling Rivers Basin locations (Yookamurra and Brookfield conservation parks) are ostensibly outside this region, however they occur in a similar agricultural setting and within the mallee vegetation community. The Murray Mallee comprises 1,836,000 hectares, of which 20% is currently remnant. As with the clearing history of the Wheatbelt, around 31% of its native vegetation was cleared by 1930, and intensive clearing occurred until the 1980s (Willoughby 2006). The Riverland Biosphere Reserve (140.600, -33.600) lies directly north of the Murray Mallee region and consists of a suite of conservation properties that were commercially grazed until the 1990’s (clearing of vegetation to create pasture was very limited). The region comprises some 900,000 hectares, and is managed by both government and not-for-profit agencies. The Flinders Ranges National Park (138.400, -32.300) is the largest mountain range in South Australia. The area is 95,000 hectares in size and its highest point is 1,170m. Located in an area of otherwise low relief, the Flinders Ranges are proposed to act as a refugium, particularly for birds, during climatically extreme periods (Byrne 2008a).

_Sample collection and microsatellite genotyping_

Individual birds were trapped using a 9 m long, 38 mm mesh size mist-net and playback of territorial vocalisations broadcast from a small speaker adjacent to the mist-net. A 28 gauge needle was used to draw a small amount (~5µl) of blood from each bird. Blood was captured using Whatman’s® FTA elute cards and stored at room temperature with silica. DNA extraction was carried out in accordance with the procedure specified by Whatman®. The DNA was stored at -20 ºC.

_Data analysis_

Genotypes for each combination of locus and population (defined here as each sampling location) were tested for linkage disequilibrium (Lewontin and Kojima 1960) and assessed for departures from Hardy-Weinberg equilibrium (Guo and Thompson 1992) using ARLEQUIN 3.5.1.2 (Excoffier and Lischer 2010). Deviations from Hardy-Weinberg equilibrium (HWE) can be due to population level processes such as subpopulation structure (Wahlund effect), inbreeding, or due to the presences of
null (non-amplified) alleles. The presence of null alleles is known to have a strong effect on genotype-based statistics such as $F_{IS}$. Therefore as a secondary check of the loci’s deviating from HWE we calculated $F_{IS}$ for each locus. The sequential Bonferroni procedure (Rice 1989) was applied to adjust significance levels ($\alpha = 0.05$). MICRO-CHECKER was utilised to check for allele scoring errors due to stuttering and large allele drop out (Van Oosterhout et al. 2004). To calculate a genotyping error, we repeat-genotyped approximately 11% of samples for each marker, and calculated scoring errors per allele and per reaction for each locus and summarised across all loci (*sensu* Hoffman and Amos 2005).

Genetic diversity was calculated for each location as observed ($H_{o}$) and expected ($H_{e}$) heterozygosity (Nei 1978), as well as the inbreeding coefficient $F_{IS}$ to examine for population substructure (Wier and Cockerham 1984) using ARLEQUIN. Additionally, allelic richness ($AR$) and the number of private alleles ($PA$) were calculated using a rarefaction approach (Hurlbert 1971, Petit et al. 1998, Kalinowski 2004) in the program ADZE (Szpiech et al. 2008). The rarefaction method ensures that the impact of unequal sample sizes on parameter estimates is alleviated by standardising all sample sizes so that each are equal to or less than the smallest sample size. The statistical significance of differences in genetic diversity between regions was calculated using FSTAT v2.9.3.2 (Goudet 1995).

We assess the abundant centre hypothesis using regression analyses between latitude and measures of within sampling location genetic diversity. Latitude is a good surrogate for proximity to range margins for the southern scrub-robin’s range across the breadth of our sampling locations. At lower latitudes (north) the scrub-robin’s range is narrow such that sampling locations are close to range margins. At higher latitudes (south) the scrub robin’s range broadens and sampling locations are increasingly distant from range margins.

Levels of genetic diversity among sampling locations was estimated with hierarchical analysis of molecular variance (AMOVA) (Excoffier et al. 1992) and pairwise $F_{ST}$ measures (Wier and Cockerham 1984) using ARLEQUIN. The sequential Bonferroni procedure (Rice 1989) was applied to
adjust significance levels ($\alpha = 0.05$). We also calculated a recently developed measure of pairwise population differentiation, $D_{\text{EST}}$ (Jost 2008), which avoids the dependence on the level of genetic variation inherent in pairwise $F_{ST}$ estimates when using highly polymorphic markers such as microsatellites (Hedrick 2005, Jost 2008, Heller and Siegismund 2009). We employed the online software SMOGD (Crawford 2010) to calculate pairwise $D_{\text{EST}}$ estimates, using 1000 bootstrap replicates. Reported values are the harmonic means across all loci, following Heller et al. (2010). The likelihood of genetic differentiation due to distance between samples (isolation by distance) was calculated using a Mantel test (Mantel 1967) implemented within the program ARLEQUIN. We calculated effective population size ($N_e$) using ONeSAMP (Tallmon et al. 2008), implemented via an online software interface (Koyuk et al. 2011). ONeSAMP infers effective population size from summary statistics calculated using microsatellite data within an approximate Bayesian framework. Onesamp creates 50,000 simulated populations on the basis of user inputs, each of which has an effective size drawn from a uniform random number between the lower and upper $N_e$ specified as priors by the user (Tallmon et al. 2008). We specified a range for $N_e$ of two to 200 for natural populations, and two to 100 for remnant populations under the assumption that remnant populations are smaller due to less available habitat and greater isolation. However preliminary testing revealed that the dataset was robust to changes in priors (up to a range of two to 1000).

Patch size was derived using the National Vegetation Information System (NVIS) raster layer for extant vegetation (cell size 100 m x 100 m), provided by Australian Government’s Department of the Environment and Water Resources (DEWR 2006). Data for this raster layer were compiled from a variety of state based sources, and were collected on ground between 1997 and 2004. We reclassified all vegetation categories into a single native vegetation class, and the raster layer was converted to a polygon shape file, which allowed an area calculation for each polygon using ArcGIS® (version 9.3.1, ESRI). Sample location centroids were calculated as the mean of Universal Transverse Mercator capture coordinates at each location. Each location centroid was then used to identify the native vegetation patch in which that population was situated, and the area of that patch. Patches were not always distinct (occasionally they were joined by a very narrow vegetated strip to other vegetated areas), however we believe our approach is the best method to
quantifying area of available habitat. We also used location centroids to extract information from the Birds Australia compilation of survey reporting rates (%) as a surrogate for population size (Barrett et al. 2003) (supplementary section).

The Bayesian clustering algorithm STRUCTURE, version 2.3.3 (Pritchard et al. 2000), was used to infer number of population clusters and identify admixed individuals using sampling location as prior information in its analysis (LOCPRIOR model). The LOCPRIOR model within STRUCTURE preferentially creates clusters that reflect sampling locations, but disregards sampling information if it proves to be uninformative about the ancestry of individuals (Hubisz et al. 2009). LOCPRIOR is a more accurate clustering approach when population structure is weak, which was evident in our dataset as low observed $F_{ST}$ and $D_{EST}$ values. Initially we employed STRUCTURE using all 17 sample locations, for 10 independent runs of each $K$ (number of genetically defined population clusters based on admixture proportions), between 1 and 17 using 1,000,000 Markov chain Monte Carlo (MCMC) interactions and a burn-in period of 100,000 steps. Furthermore, as STRUCTURE only detects the uppermost level of genetic structure within a given dataset, we employed a hierarchical approach to investigate substructure within each identified cluster following Roux et al. (2010). For each substructure group, we estimated the number of genetic clusters by performing 10 independent runs of each $K$ between 1 and the number of sample locations plus two, using 1,000,000 MCMC interactions and a burn-in period of 100,000 steps.

In order to determine the true number of clusters ($K$), we estimated $\Delta K$ based on the rate of change in the log probability of data between successive $K$ values following Evanno et al. (2005), as implemented by the online program Structure Harvester (Earl 2011). Subsequently we employed the FullSearch algorithm within the CLUster Matching and Permutation Program 1.1.2 (CLUMPP) (Jakobsson and Rosenberg 2007) to determine the optimal alignment for the 10 replicate runs of the appropriate $K$ value. The proportion of cluster membership within each sample site was determined, with individuals being assigned to a cluster when the probability was $> 0.7$. Output from CLUMPP was used in the program Distruct (Rosenberg 2004), in order to produce a graphical display of the permuted matrices.
Recent bidirectional migration rates per generation were estimated using BayesAss+ (Wilson and Rannala 2003). BayesAss+ calculates gene flow based upon the migration rate within the last one to three generations. Estimates are most accurate under conditions of low migration rate and high population genetic differentiation (Wilson and Rannala 2003). Delta values for allele frequencies, inbreeding coefficients and migration rates were amended to maximise the final total log likelihood and obtain acceptance rates of 40-60%, suggested as best practice by the program authors (Wilson and Rannala 2003). In order to minimise the possibility of convergence problems with the MCMC chains identified in Faubet et al.’s (2007) simulation study, we followed their suggestions and performed 10 MCMC runs, using initial seeds from one through to ten. Each MCMC run consisted of $21 \times 10^6$ iterations, discarding the first $2 \times 10^6$ as burn in after which data were collected every 2000 iterations to infer population allele frequencies and the proportion of migrants. To estimate model fit for each run, we calculated Bayesian deviance as described by Faubet et al. (2007). Results reported in this paper represent the migration estimates from the model with the lowest Bayesian deviance.

**Results**

*Evaluating loci*

Regenotyping of samples revealed scoring errors for loci DRYB15 (0.0167 per reaction, 0.0083 per allele), DRYB29 (0.0323 per reaction, 0.0161 per allele) and DRYB34 (0.0172 per reaction, 0.0086 per allele). Summarised across all loci, this equates to an error rate per reaction of 0.0071 and 0.0036 per allele. We found no evidence of scoring errors due to large allele drop-out or stuttering. Deviations from Hardy-Weinberg equilibrium at four loci (DRYB15, DRYB21, DRYB29, DRYB34) were evident at single sampling localities. We found that locus DRYB21 had an FIS value of more than double that of any other locus. On the basis of these combined results, we eliminated locus DRYB21 from further analysis due to the probable presence of null alleles. All other loci were included in analyses. Linkage disequilibrium was detected for 5 locus pairs, comprising just 0.82%
of total pairs assessed (36 locus comparisons for each of 17 populations). Because no one pair of loci was found to be in linkage disequilibrium (LD) in more than one sampling location, we attributed this result to population-specific genetic processes and no loci were excluded due to LD.

Patch size

Most sampling locations (seven in South Australia and three in Western Australia) were within a large area of contiguous native vegetation that forms the rangelands of central Australia (Table 4.1). In the Murray Mallee, HB occupied the smallest patch of native vegetation, while BS and BN were both located in Billiatt Conservation Park, of the largest remnant native vegetation patch in South Australia. Both YS and BR were located in a patch connected to the large area of contiguous native vegetation found in central Australia by a narrow corridor. In the Western Australian Wheatbelt, CG was located in the smallest patch of native vegetation for the entire study, while the sample site DR was found within the largest patch of remnant vegetation.

Genetic diversity

The number of alleles per locus ranged from four (DRYB46) to 17 (DRYB 33), (mean and std dev = 10.11 ± 3.54) (Table 4.1). All loci in all sampling locations were polymorphic. Levels of genetic diversity (as estimated by $H_e$ and $AR$) showed non-significant differences ($H_e$: p = 0.727; $AR$: p = 0.282) between the Wheatbelt in Western Australia and regions within South Australia (average values; $H_e$: Western Australia 0.674, South Australia 0.680, $AR$: Western Australia 3.996, South Australia 3.843). Average $F_{IS}$ values indicate a significant difference (p = 0.006) between an excess of heterozygotes in Western Australia (-0.024), and a deficiency of heterozygotes in South Australia (0.078). Conversely, genetic diversity did vary considerably within each state. In Western Australia, CG, the population with the smallest patch size had the lowest levels of genetic diversity ($H_e = 0.569$ and $AR = 3.181$) (Table 4.1). Dragon Rocks NR, the southernmost sampling location in Western Australia, had the highest levels of genetic diversity ($H_e = 0.755$ and $AR = 4.711$). Population substructure was generally low across the state; FP had the highest $F_{IS}$ value (-0.083).
Figure 4.1 Spatial location and Structure cluster assignments for sampled locations as indicated by pane titles. The left pane gives an overview of the sampling structure across Australia, and Structure results indicate initial sample location cluster assignment. The central and right panes show Western Australia and South Australian sample locations respectively and detail individual scrub-robin assignment to Structure clusters within each location determined during substructure (secondary) analysis. The Wheatbelt region (receiving between 280 and 600 mm of rainfall annually, in aqua) is outlined in Western Australia. In South Australia, the Flinders ranges (orange) Murray-Darling Rivers Basin (red), Riverland Biosphere Reserve (green) and Murray Mallee (pink) are outlined.
Table 4.1 Genetic indices at 9 microsatellite loci in 12 South Australian (above line), and 5 Western Australian (below line) sampling locations. Each location is detailed with its name and abbreviation, number of birds sampled ($N$), patch size (hectares), reporting rate (%), effective population size ($Ne$), upper (UCI) and lower (LCI) 95% confidence intervals, observed ($Ho$) and expected ($He$) heterozygosities, fixation index ($F_{IS}$), allelic richness ($AR$) and private alleles ($PA$).

<table>
<thead>
<tr>
<th>Location</th>
<th>Abbreviation</th>
<th>$N$</th>
<th>Patch size</th>
<th>Reporting rate (%)</th>
<th>$Ne$</th>
<th>$Ho$</th>
<th>$He$</th>
<th>$F_{IS}$</th>
<th>$AR$</th>
<th>$PA$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arkaroo Rock</td>
<td>AR</td>
<td>17</td>
<td>contiguous</td>
<td>&gt;0</td>
<td>19.006 (14.458, 33.882 )</td>
<td>0.497</td>
<td>0.595</td>
<td>0.156</td>
<td>3.237</td>
<td>0.083</td>
</tr>
<tr>
<td>Telowie Gorge</td>
<td>TG</td>
<td>17</td>
<td>contiguous</td>
<td>&gt;0</td>
<td>18.899 (15.557, 29.941)</td>
<td>0.600</td>
<td>0.612</td>
<td>0.012</td>
<td>3.561</td>
<td>0.026</td>
</tr>
<tr>
<td>Yookamurra Sanctuary</td>
<td>YM</td>
<td>18</td>
<td>contiguous $^a$</td>
<td>5</td>
<td>30.098 (23.300, 57.741)</td>
<td>0.618</td>
<td>0.690</td>
<td>0.087</td>
<td>3.943</td>
<td>0.115</td>
</tr>
<tr>
<td>Brookfield CP</td>
<td>BR</td>
<td>11</td>
<td>contiguous $^a$</td>
<td>5</td>
<td>12.321 (9.200, 20.668)</td>
<td>0.545</td>
<td>0.671</td>
<td>0.195</td>
<td>3.749</td>
<td>0.072</td>
</tr>
<tr>
<td>Henry's Block</td>
<td>HB</td>
<td>18</td>
<td>22728</td>
<td>5</td>
<td>21.353 (16.318, 44.303)</td>
<td>0.569</td>
<td>0.673</td>
<td>0.146</td>
<td>3.660</td>
<td>0.070</td>
</tr>
<tr>
<td>Froggy Dam</td>
<td>FD</td>
<td>17</td>
<td>contiguous</td>
<td>10</td>
<td>21.265 (17.194, 33.491)</td>
<td>0.660</td>
<td>0.704</td>
<td>0.064</td>
<td>3.956</td>
<td>0.024</td>
</tr>
<tr>
<td>Long Dam</td>
<td>LD</td>
<td>18</td>
<td>contiguous</td>
<td>10</td>
<td>20.238 (15.825, 32.496)</td>
<td>0.630</td>
<td>0.690</td>
<td>0.090</td>
<td>3.850</td>
<td>0.043</td>
</tr>
<tr>
<td>Taylorville Station</td>
<td>TS</td>
<td>16</td>
<td>contiguous</td>
<td>10</td>
<td>18.669 (15.118, 32.754)</td>
<td>0.632</td>
<td>0.709</td>
<td>0.112</td>
<td>3.945</td>
<td>0.073</td>
</tr>
<tr>
<td>Hideaway Block</td>
<td>HD</td>
<td>18</td>
<td>contiguous</td>
<td>10</td>
<td>23.918 (18.728, 46.792)</td>
<td>0.668</td>
<td>0.700</td>
<td>0.034</td>
<td>3.938</td>
<td>0.099</td>
</tr>
<tr>
<td>Billiatt CP South</td>
<td>BS</td>
<td>22</td>
<td>101209</td>
<td>20</td>
<td>33.128 (25.707, 58.358)</td>
<td>0.662</td>
<td>0.728</td>
<td>0.094</td>
<td>4.297</td>
<td>0.153</td>
</tr>
<tr>
<td>Billiatt CP North</td>
<td>BN</td>
<td>16</td>
<td>101209</td>
<td>20</td>
<td>19.625 (17.000, 28.031)</td>
<td>0.736</td>
<td>0.717</td>
<td>-0.027</td>
<td>4.156</td>
<td>0.052</td>
</tr>
<tr>
<td>Dangalli CP</td>
<td>DG</td>
<td>19</td>
<td>contiguous</td>
<td>10</td>
<td>22.693 (19.620, 31.694)</td>
<td>0.690</td>
<td>0.674</td>
<td>-0.025</td>
<td>3.820</td>
<td>0.011</td>
</tr>
<tr>
<td>Dragon Rocks NR</td>
<td>DR</td>
<td>16</td>
<td>33295</td>
<td>30</td>
<td>15.378 (12.614, 25.866)</td>
<td>0.734</td>
<td>0.755</td>
<td>0.013</td>
<td>4.711</td>
<td>0.233</td>
</tr>
<tr>
<td>Charles Gardner NR</td>
<td>CG</td>
<td>16</td>
<td>653</td>
<td>&gt;0</td>
<td>23.340 (18.949, 37.254)</td>
<td>0.569</td>
<td>0.574</td>
<td>0.008</td>
<td>3.181</td>
<td>0.076</td>
</tr>
<tr>
<td>Mt Gibson Sanctuary</td>
<td>MG</td>
<td>14</td>
<td>contiguous</td>
<td>5</td>
<td>15.696 (13.389, 22.174)</td>
<td>0.742</td>
<td>0.730</td>
<td>-0.030</td>
<td>4.412</td>
<td>0.173</td>
</tr>
<tr>
<td>Kalbarri NP</td>
<td>KB</td>
<td>14</td>
<td>contiguous</td>
<td>5</td>
<td>14.162 (11.933, 20.422)</td>
<td>0.685</td>
<td>0.672</td>
<td>-0.028</td>
<td>3.816</td>
<td>0.165</td>
</tr>
<tr>
<td>Francois Peron NP</td>
<td>FP</td>
<td>14</td>
<td>contiguous</td>
<td>20</td>
<td>19.170 (15.401, 30.124)</td>
<td>0.688</td>
<td>0.642</td>
<td>-0.083</td>
<td>3.860</td>
<td>0.231</td>
</tr>
</tbody>
</table>
In South Australia levels of genetic diversity were significantly lower in conservation parks. This trend was predominately driven by the Flinders ranges, whose levels of genetic diversity (average values for \( H_e \) 0.604, and \( AR \) 3.399) were significantly lower (\( H_e \); \( p = 0.016 \); \( AR \); \( p = 0.031 \)) than those in the Murray-Darling Rivers Basin region (average values for \( H_e \) 0.696, and \( AR \) 3.931).

Indeed, within South Australia there is a strong negative relationship between latitude and genetic diversity (Figure 4.2). Similar trends also exist in Western Australia when CG is excluded. However, the highest levels of inbreeding (population substructure) were also found in the agricultural Murray Mallee (average \( F_{IS} \); 0.099) although there was no significant difference (\( p = 0.701 \)) to inbreeding in the Riverland Biosphere Reserve (average \( F_{IS} \); 0.055) and the Flinders Ranges (average \( F_{IS} \); 0.084).

*Effective population size*

The highest \( Ne \) values were in the southern areas of both Western Australia and South Australia. In South Australia the highest effective population sizes were within the Murray Mallee, at YS (\( Ne = 30.098, 95\% \) CI = 23.300, 57.741) and BS (\( Ne = 33.128, 95\% \) CI = 25.707, 58.358). The smallest \( Ne \) value was also within the Murray Mallee, at BR (\( Ne = 12.321, 95\% \) CI = 9.200, 20.668). Inbreeding demonstrates a negative correlation with effective populations size (Figure 4.3). Conversely effective population size demonstrated a positive correlation with latitude (\( y = -2.0315x - 47.045, R^2 = 0.122 \)), and the reporting rate of southern scrub-robin (Figure 4.4). In Western Australia, the most isolated sampling location, CG, had the highest effective population size (\( Ne = 23.340, 95\% \) CI = 18.949, 37.254), followed by the northern-most location FP (\( Ne = 19.17, 95\% \) CI = 15.401, 30.124). The reporting rate for southern scrub-robins and latitude do not show the same relationships with \( Ne \) in Western Australia as demonstrated in South Australia. Charles Gardener has a very low reporting rate (\( > 0 \% \), the lowest value), while DR has the highest reporting rate for Western Australia (30\%) and one of the smallest effective population sizes (\( Ne = 15.378, 95\% \) CI =12.614, 25.866).
Figure 4.2 Measures of genetic diversity and differentiation (Y-axis) for locations sampled in South Australia plotted against latitude (X-axis).
Figure 4.3 Inbreeding co-efficient (Y-axis) for locations sampled in South Australia plotted against effective population size (X-axis).

Figure 4.4 Effective population size (Y-axis) for locations sampled in South Australia plotted against reporting rate for southern scrub-robins obtained from Birds Australia atlas data (X-axis).
STRUCTURE clearly identified two clusters concordant with each state (Figure 4.1). Each population had a mean probability of cluster assignment > 0.79. Subsequently we investigated substructure within both Western and South Australia (Figure 4.1). Within Western Australia, a further two clusters were identified. Charles Gardener CP, the location most highly isolated by the agricultural matrix, was identified as separate from the remaining four sampled locations (FP, KB, MG and DR). Mean individual assignment probability to clusters was high in both cluster one (CG = 0.99 ± 0.009) and cluster two (FP = 0.99 ± 0.002, KB = 0.98 ± 0.009, MG = 0.98 ± 0.031 and DR = 0.91 ± 0.064). All individuals had a mean assignment probability of > 0.7. In South Australia, three geographically structured clusters were identified. Locations within the Murray Mallee were not separated from those in the contiguous vegetation directly north. Mean individual assignment probability to clusters was high in clusters one and (AR = 0.93 ± 0.046) and three (HB = 0.95 ± 0.016, FD = 0.79 ± 0.088, LD = 0.97 ± 0.022, TS = 0.79 ± 0.103, HD = 0.76 ± 0.097, BS = 0.84 ± 0.052, BN = 0.86 ± 0.102, and DG = 0.92 ± 0.040). One individual from FD, two from TS, one for HD and one from BN had a mean assignment probability of < 0.7. The individual from HD had the greatest assignment probability for cluster one. Cluster two was comprised of three sampling locations, two of which were highly admixed (TG = 0.92 ± 0.032, YM = 0.54 ± 0.087 and BR = 0.43 ± 0.094). Five individuals each from YM and BR had a higher assignment probability for cluster three than for cluster two. None of the individuals from YM or BR had a mean assignment probability of > 0.7.

Genetic differentiation

Genetic differentiation as calculated by pairwise $F_{ST}$ and $D_{EST}$ both reflect a similar pattern in South Australia (Table 4.2). Pairwise estimates of $D_{EST}$ were on average only 0.006 greater than pairwise
Table 4.2 Pairwise $D_{EST}$ (above the diagonal) and $F_{ST}$ (below the diagonal) estimates for 12 South Australian sampling locations. Pairwise $F_{ST}$ estimates underlined retain statistical significance after the sequential Bonferroni correction was applied.

<table>
<thead>
<tr>
<th></th>
<th>AR</th>
<th>TG</th>
<th>YS</th>
<th>BR</th>
<th>HB</th>
<th>FD</th>
<th>LD</th>
<th>TS</th>
<th>HD</th>
<th>BS</th>
<th>BN</th>
<th>DG</th>
</tr>
</thead>
<tbody>
<tr>
<td>AR</td>
<td>—</td>
<td>0.164</td>
<td>0.126</td>
<td>0.214</td>
<td>0.166</td>
<td>0.101</td>
<td>0.197</td>
<td>0.104</td>
<td>0.083</td>
<td>0.210</td>
<td>0.189</td>
<td>0.132</td>
</tr>
<tr>
<td>TG</td>
<td>0.180</td>
<td>—</td>
<td>0.033</td>
<td>0.100</td>
<td>0.132</td>
<td>0.064</td>
<td>0.153</td>
<td>0.160</td>
<td>0.098</td>
<td>0.074</td>
<td>0.073</td>
<td>0.171</td>
</tr>
<tr>
<td>YS</td>
<td>0.126</td>
<td>0.052</td>
<td>—</td>
<td>0.107</td>
<td>0.054</td>
<td>0.034</td>
<td>0.078</td>
<td>0.049</td>
<td>0.006</td>
<td>0.017</td>
<td>0.034</td>
<td>0.088</td>
</tr>
<tr>
<td>BR</td>
<td>0.157</td>
<td>0.125</td>
<td>0.075</td>
<td>—</td>
<td>0.039</td>
<td>0.069</td>
<td>0.114</td>
<td>0.114</td>
<td>0.061</td>
<td>0.045</td>
<td>0.051</td>
<td>0.080</td>
</tr>
<tr>
<td>HB</td>
<td>0.137</td>
<td>0.118</td>
<td>0.051</td>
<td>0.052</td>
<td>—</td>
<td>0.034</td>
<td>0.061</td>
<td>0.062</td>
<td>0.025</td>
<td>0.005</td>
<td>0.000</td>
<td>0.005</td>
</tr>
<tr>
<td>FD</td>
<td>0.108</td>
<td>0.044</td>
<td>0.040</td>
<td>0.060</td>
<td>0.036</td>
<td>—</td>
<td>0.008</td>
<td>0.061</td>
<td>0.008</td>
<td>0.011</td>
<td>0.009</td>
<td>0.018</td>
</tr>
<tr>
<td>LD</td>
<td>0.153</td>
<td>0.141</td>
<td>0.081</td>
<td>0.076</td>
<td>0.053</td>
<td>0.035</td>
<td>—</td>
<td>0.034</td>
<td>0.016</td>
<td>0.016</td>
<td>0.041</td>
<td>0.043</td>
</tr>
<tr>
<td>TS</td>
<td>0.104</td>
<td>0.111</td>
<td>0.028</td>
<td>0.080</td>
<td>0.058</td>
<td>0.035</td>
<td>0.048</td>
<td>—</td>
<td>0.033</td>
<td>0.055</td>
<td>0.035</td>
<td>0.054</td>
</tr>
<tr>
<td>HD</td>
<td>0.113</td>
<td>0.080</td>
<td>0.026</td>
<td>0.048</td>
<td>0.028</td>
<td>0.017</td>
<td>0.030</td>
<td>0.020</td>
<td>—</td>
<td>0.003</td>
<td>0.028</td>
<td>0.024</td>
</tr>
<tr>
<td>BS</td>
<td>0.130</td>
<td>0.077</td>
<td>0.020</td>
<td>0.055</td>
<td>0.012</td>
<td>0.023</td>
<td>0.024</td>
<td>0.029</td>
<td>0.007</td>
<td>—</td>
<td>0.000</td>
<td>0.026</td>
</tr>
<tr>
<td>BN</td>
<td>0.127</td>
<td>0.097</td>
<td>0.032</td>
<td>0.051</td>
<td>0.001</td>
<td>0.023</td>
<td>0.030</td>
<td>0.030</td>
<td>0.028</td>
<td>-0.001</td>
<td>—</td>
<td>0.000</td>
</tr>
<tr>
<td>DG</td>
<td>0.121</td>
<td>0.115</td>
<td>0.067</td>
<td>0.070</td>
<td>0.013</td>
<td>0.031</td>
<td>0.045</td>
<td>0.045</td>
<td>0.025</td>
<td>0.022</td>
<td>0.008</td>
<td>—</td>
</tr>
</tbody>
</table>

Table 4.3 Pairwise $D_{EST}$ (above the diagonal) and $F_{ST}$ (below the diagonal) estimates for 5 Western Australian sampling locations. Pairwise $F_{ST}$ estimates underlined retain statistical significance after the sequential Bonferroni correction was applied.

<table>
<thead>
<tr>
<th></th>
<th>FP</th>
<th>KB</th>
<th>MG</th>
<th>CG</th>
<th>DR</th>
</tr>
</thead>
<tbody>
<tr>
<td>FP</td>
<td>—</td>
<td>0.174</td>
<td>0.098</td>
<td>0.234</td>
<td>0.098</td>
</tr>
<tr>
<td>KB</td>
<td>0.105</td>
<td>—</td>
<td>0.097</td>
<td>0.175</td>
<td>0.094</td>
</tr>
<tr>
<td>MG</td>
<td>0.062</td>
<td>0.066</td>
<td>—</td>
<td>0.183</td>
<td>0.011</td>
</tr>
<tr>
<td>CG</td>
<td>0.190</td>
<td>0.159</td>
<td>0.135</td>
<td>—</td>
<td>0.167</td>
</tr>
<tr>
<td>DR</td>
<td>0.066</td>
<td>0.058</td>
<td>0.008</td>
<td>0.118</td>
<td>—</td>
</tr>
</tbody>
</table>

$F_{ST}$ estimates. In Western Australia, $D_{EST}$ estimates were consistently higher, on average 0.036 greater than the same $F_{ST}$ comparison.

AMOVA results indicate that within South Australia among population differentiation is low ($F_{ST} = 0.06001$). This result is supported by low levels of $PA$ across South Australia (Table 4.1). Pairwise $F_{ST}$ and $D_{EST}$ values suggest genetic differentiation is highest between populations in the Flinders Ranges and the Murray-Darling Rivers Basin. Genetic differentiation among the Riverland Biosphere Reserve and Murray Mallee regions is low.
Table 4.4 Recent migration estimates (95% confidence intervals in brackets) from and into each of 3 South Australian Structure groups derived using BayesAss+. Estimates bolded along the diagonal represent the proportion of individuals which did not migrate away from their natal site each generation. Structure group one includes only population AR, group two includes populations TG, YS and BR, group three contains all remaining populations (HB, FD, LD, TS, HD, BS, BN and DG).

<table>
<thead>
<tr>
<th>from/into</th>
<th>ONE</th>
<th>TWO</th>
<th>THREE</th>
</tr>
</thead>
<tbody>
<tr>
<td>ONE</td>
<td>0.972 (0.913, 0.999)</td>
<td>0.01 (0.000, 0.038)</td>
<td>0.007 (0.000, 0.021)</td>
</tr>
<tr>
<td>TWO</td>
<td>0.012 (0.000, 0.058)</td>
<td>0.779 (0.708, 0.878)</td>
<td>0.005 (0, 0.017)</td>
</tr>
<tr>
<td>THREE</td>
<td>0.015 (0.000, 0.061)</td>
<td>0.211 (0.112, 0.283)</td>
<td>0.988 (0.970, 0.999)</td>
</tr>
</tbody>
</table>

Table 4.5 Recent migration estimates (95% confidence intervals in brackets) from and into each population derived using BayesAss+ for five Western Australian sampling locations. Estimates bolded along the diagonal represent the proportion of individuals which did not migrate away from their natal site each generation.

<table>
<thead>
<tr>
<th>from/into</th>
<th>DR</th>
<th>CG</th>
<th>MG</th>
<th>KB</th>
<th>FP</th>
</tr>
</thead>
<tbody>
<tr>
<td>DR</td>
<td>0.725 (0.668, 0.869)</td>
<td>0.005 (0, 0.032)</td>
<td>0.058 (0, 0.242)</td>
<td>0.006 (0, 0.035)</td>
<td>0.007 (0, 0.036)</td>
</tr>
<tr>
<td>CG</td>
<td>0.029 (0, 0.108)</td>
<td>0.981 (0.93, 0.999)</td>
<td>0.019 (0, 0.077)</td>
<td>0.006 (0, 0.037)</td>
<td>0.006 (0, 0.04)</td>
</tr>
<tr>
<td>MG</td>
<td>0.182 (0.036, 0.306)</td>
<td>0.005 (0, 0.029)</td>
<td>0.823 (0.679, 0.979)</td>
<td>0.006 (0, 0.039)</td>
<td>0.008 (0, 0.052)</td>
</tr>
<tr>
<td>KB</td>
<td>0.02 (0, 0.093)</td>
<td>0.005 (0, 0.031)</td>
<td>0.074 (0, 0.206)</td>
<td>0.972 (0.905, 0.999)</td>
<td>0.009 (0, 0.053)</td>
</tr>
<tr>
<td>FP</td>
<td>0.045 (0, 0.163)</td>
<td>0.005 (0, 0.033)</td>
<td>0.025 (0, 0.129)</td>
<td>0.009 (0, 0.05)</td>
<td>0.969 (0.888, 0.999)</td>
</tr>
</tbody>
</table>
Isolation by distance (Mantel test) estimates indicate that distance is responsible for 51% (correlation coefficient = 0.714908, p = 0.005000) of genetic structure as measured by pairwise $F_{ST}$ in South Australia.

In Western Australia, among population differentiation is higher than in South Australia ($F_{ST} = 0.09786$). Genetic differentiation between populations as measured by pairwise $F_{ST}$ is high, except for MG sanctuary, situated centrally to other populations. Charles Gardener NR has the highest pairwise $F_{ST}$ and $D_{EST}$ values. These results are supported by relatively high PA values across Western Australian sampling locations (Table 4.1), except in the case of CG which has a low PA value (0.076). Isolation by distance (mantel test) indicates that distance has very little influence on genetic structure (0.000087%, correlation coefficient = -0.009307, p = 0.477000).

Recent Migration

We report migration rates between STRUCTURE designations rather than sampling locations for South Australia due to low observed population structure. When estimating recent migration rates using BayesASS+ among locations that have pairwise $F_{ST}$ values less than 0.05, a large proportion of individuals can be misassigned to a source population (Faubet et al. 2007). Despite a high certainty attributed to assignments, many populations have approximately 2/3 non migrant individuals (close to the lower bound of the prior distribution for $m$), and most migrants are attributed to a single population with a low immigration rate (Faubet et al. 2007). This is the scenario we observed when we attempted to estimate migration between sampling locations in South Australia, where 47% of all pairwise $F_{ST}$ values fall below 0.05. We therefore decided to pool data according the population clusters proposed by STRUCTURE and estimate migration between these clusters.

Sample localities were pooled in South Australia into Structure clusters one (AR), two (TG, YS and BR) and three (HB, FD, LD, TS, HD, BS, BN and DG). Results indicate that there are only very small
levels of gene flow between these population clusters (Table 4.4). The exception is that approximately 21% of individuals in cluster two originate from cluster three.

In Western Australia, migration rates were derived between sampling locations, as population structure was sufficient for reliable estimation (Table 4.5). In Western Australia, migration was also low. Charles Gardener NP, Kalbarri NP and Francois Peron NP have a high percentage of non-migrant individuals (≥ 96%). Mt Gibson Sanctuary received small numbers of migrants from other sampled populations (between 1.9 and 7.4%), while DR receives some 18.2% of its immigrants from MG (or other stepping-stone populations with which they both have gene flow).

**Discussion**

Protected area networks are frequently based upon unsuitability for agriculture or urbanization, and rarely consider the demographic characteristics of the species they purportedly protect (Fuller et al. 2010). Consequently, habitat protection frequently occurs on the fringe of species’ distributions and at their upper climatic tolerances. Climate change is likely to shift many habitat envelopes away from these current mainstays of conservation. Concurrently, substantial habitat loss and erosion of genetic diversity at the core of their distribution may leave many species ill prepared to adapt to climate change. We find that at present, agriculture has neither lead to increased levels of between population diversity nor greatly decreased levels of within population diversity in the southern scrub-robin. In both regions sampling locations within the agricultural matrices contain the highest level of genetic diversity. Furthermore, low between population diversity, population clustering and levels of recent migration all indicate agricultural clearing has had a minimal impact on the microevolutionary processes of the southern scrub-robin.

*The abundant centre hypothesis*

Our results demonstrate a strong trend of increasing genetic diversity with increasing latitude such that sampling sites closer to the centre of the distribution of the southern scrub-robin have higher levels of
genetic diversity, which supports the abundant centre hypothesis. The abundant centre hypothesis (see Sagarin and Gaines 2002 for history of this concept) proposes that at the centre of a species’ distribution, conditions are optimal and hence population size and density are at their highest, whereas at the periphery of a species’ range, environmental conditions are stressful and populations are comparatively smaller and more isolated (Brown 1984, Vucetich and Waite 2003). Consequently, we would expect to see a reduction in genetic diversity and increased genetic structure in populations proximate to range margins. These predictions are reflected in the patterns of genetic diversity, gene flow and effective population size observed in both Western Australia and South Australia. Not only is genetic diversity highest in the higher latitudes of the scrub-robin’s distribution, but so is gene flow. In contrast, in Western Australia the results for effective population size were counterintuitive (CG, the site in the smallest, most isolated fragment simultaneously had the lowest level of heterozygosity and highest effective population size). In South Australia effective population size in northern sites was comparatively lower.

Despite substantial agricultural change, such that habitat conditions may no longer be optimal, the southern scrub-robin has continued to maintain larger effective population sizes and higher genetic diversity at the core of its distribution. How has this been possible? Firstly, in South Australia’s Murray Mallee, vegetation remnancy is relatively high (20%) and clearing preferentially targeted habitat types with a grassy, rather than a shrubby understorey (Willoughby 2006). Woodlands were initially targeted for agricultural clearing in Western Australia, but large scale clearing of shrublands eventually took place (Prober and Smith 2009). However in both states, sampling sites within the agricultural matrix were predominantly located in remnant vegetation proximate to, and connected with, larger tracts of native vegetation via ‘stepping stones’ of uncleared vegetation patches (Figure 4.1). This pattern suggests that while the sampling sites are located within a fragmented habitat, they might not necessarily be isolated. High levels of gene flow between subpopulations may counter the effects of reduced local population size and genetic drift potentially caused by habitat fragmentation (Keyghobadi et al. 2005). However our results suggest there may also be a time lag in detecting the effects of agriculture on genetic diversity and structure. Although habitat fragmentation has seemingly not adversely affected genetic diversity and population structure in general, southern scrub-robin’s
located in the smallest habitat fragments may well be the canary down the mine. Comparatively higher levels of population substructure (as indicated by higher $F_{IS}$ values) and reduced genetic diversity in the smallest fragments suggest the species may be on the verge of a decline in highly fragmented agricultural areas where the inbreeding coefficient is the most sensitive of these three measures to demographic changes (Lowe et al. 2005).

**Future conservation**

Southern scrub-robinbs have maintained high levels of gene flow and genetic diversity in agricultural areas, but additional pressures due to anthropogenic climate change appear likely. Protected areas for the southern scrub-robin in both Western Australia and South Australia are largely on the fringe of its distribution. Given that climate change is forecast to increase temperature and decrease precipitation in the mallee region (Holper 2007), the northern extremes of the southern scrub-robin’s distribution may become climatically unsuitable over the coming century. Consequently, large conservation areas such as the Riverland Biosphere Reserve (South Australia), and Francois Peron National Park (Western Australia) may soon become ineffective for the conservation of this, and many other semi-arid species. The Flinders Ranges in South Australia have long been hypothesised to offer climatic refugia to species in this area by virtue to their topography (Byrne 2008a). Our two Flinders Ranges sites (AR and TG) demonstrated high levels of genetic differentiation from most other South Australian sites, in conjunction with low levels of migration. Additionally, these sites had comparatively low levels of contemporary genetic diversity. It would appear for the southern scrub-robin, the Flinders Ranges are unlikely to offer a contemporary genetic refugium, even if it remains climatically suitable for the species.

Results from this study suggest populations embedded with the southern agricultural regions of both Western and South Australia are most important areas to focus on for genetic conservation, in particular where large conservation parks already occur in the region, e.g. Dragon Rocks (Western Australia) and Billiatt (South Australia). These locations maintain high levels of genetic diversity, low levels of inbreeding, and maintain gene flow with proximate areas of the southern scrub-robin’s
distribution. Importantly, because these conservation parks are not at the climatic extremes of the southern scrub-robin’s range, they are most likely to continue to offer both a suitable climate for a longer period of time into the future, and the genetic diversity necessary to adapt to climate changes over time.

Where to from here?

In addition to this body of work, we feel that an in-depth study of dispersal in southern scrub-robins is critical. Dispersal in animals is a demographic process that impacts far beyond an individual’s pursuit of fitness; it has a profound bearing on distribution, abundance and genetic structure of the metapopulation (Ricketts 2001, Prevedello and Vieira 2010). Given the relationship between dispersal and population dynamics, understanding dispersal may be considered a fundamental aspect of managing a species like the southern scrub-robin whose distribution coincides with areas of high anthropogenic activity (Bowler and Benton 2005). Studying the effect of landscape variation on gene flow would allow quantification of the impact of massive changes wrought by anthropogenic landscapes on genetic structure, and provide a basis for assessing the ability of this species to respond to any shift in habitat envelope wrought climate change. Furthermore, habitat types best suited to facilitate gene flow could be identified and used to improve restoration outcomes for this species particularly within agricultural areas in the south of their distribution that are more likely to remain climatically suitable into the future. Dispersing individuals also assess patch quality as they move through the landscape searching for a home site (Doerr et al. 2006). Patch characteristics influence whether a migrant chooses to settle, is able to find a mate, successfully reproduce and raise offspring (Johnson 2007). Patch quality is often compromised in fragmented systems due to decreased patch size and connectivity, increased amount of edge, the invasion of pest species and loss of biodiversity (Mortelliti et al. 2010, Ford 2011). However some of these effects may also be felt in areas of contiguous vegetation due to commercial and feral grazing, and poor control of weeds and other invasive species (Hobbs et al. 2008). Identifying habitat characteristics associated with large, genetically diverse populations will give conservation practitioners the knowledge to rehabilitate other areas occupied by southern scrub-robins which may be acting as population sinks (Pulliam 1988). A
further, important area of research would be that of testing whether environmental gradients drive morphological and genetic diversity. To give the southern scrub-robin the best possible chance of adapting in situ to ongoing climate change, identifying and protecting such gradients into the future will be a key conservation priority (Thomassen et al. 2010, Sgro et al. 2011).

**Conclusion**

The impact of agriculture on the genetic diversity and metapopulation structure of the southern scrub-robin in Western and South Australia appears to have been minimal to date, although southern scrub-robins continue to disappear from the smallest agricultural fragments. Genetic diversity has probably been maintained due to large fragment size and the maintenance of gene flow between remnant patches and large tracts of native vegetation in the rangelands. However, increased levels of population substructure and reduced genetic diversity in the smallest fragments suggest the species may be on the verge of a decline. In accordance with the abundant centre hypothesis, we found that locations at lower latitudes distant from range margins of this species’ distribution have higher levels of genetic diversity, and in South Australia, higher effective population size. It appears that the Flinders Ranges in South Australia are unlikely to play a refugial role for this species.

While this species persists in high numbers, its distribution in the south has undoubtedly undergone a drastic reduction where it coexists with agricultural production. With climate change threatening the viability of populations, especially those in the north of its distribution, the southern scrub-robin may well find itself stuck between a rock and a hard place. Protected areas at present are poorly placed to protect this species against the twin threats of habitat clearing and climate change. This is likely to be the case for many other species, particularly those who are mallee endemics. The reserve system in Australia requires a strategic overhaul that places biodiversity, climate change mitigation and the maintenance of genetic diversity at the core of its ethos, rather than simply accepting landscapes considered unproductive by agriculture. Ongoing monitoring of the spatial distribution and understanding of the drivers of genetic diversity, and continued research into the dispersal processes within this species will be required to ensure appropriate management and future survival.
Acknowledgements

We acknowledge the assistance and support of Kathy Saint from the University of Adelaide and Alison Fitch from Flinders University. This project was funded by CSIRO (Climate Adaptation Flagship), Department of Environment and Natural Resources in South Australia (Wildlife Conservation Fund), Sir Mark Mitchell Research Foundation, Birds Australia (Stuart Leslie Bird Research Award) and Australian Geographic Society.
Figure 4S.1. Reporting rate of the southern scrub-robin from Birds Australia atlas surveys. Reporting rate indicates the percentage of surveys in which the southern scrub-robin was detected, using black circles of increasing size to indicate increasing percentages. Figure modified that present in Barret et al. (2003).
Chapter 5:

Dispersal through the understorey: characterising genetic connectivity of the southern scrub-robin (*Drymodes burnneopygia*) in response to historical and contemporary landscapes

Jolene Scoble¹,², David Charles Pavlacky, Jr.³, Peter Cale⁴, Michael George Gardner¹,⁵, Anita Smyth⁶ and Andrew John Lowe¹,⁶,⁷*

¹ Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, North Terrace, Adelaide, SA 5005, Australia.
² CSIRO, Climate Adaptation Flagship, GPO Box 1700, Canberra, ACT 2601, Australia.
³ Rocky Mountain Bird Observatory, P. O. Box 1232, Brighton, CO 80601, USA
⁴ Australian Landscape Trust, Calperum Station, PO Box 955, Renmark SA 5341
⁵ School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide 5001, Australia
⁶ Eco-informatics Facility, Terrestrial Ecosystem Research Network, University of Adelaide, North Terrace, SA 5005, Australia.
⁷ State Herbarium of South Australia, Science Resources Centre, Department of Environment and Natural Resources, Adelaide, SA 5005, Australia.

*Corresponding author: andrew.lowe@adelaide.edu.au

Running head: bird genetic connectivity across Australian landscapes

Article type: Empirical research
STATEMENT OF AUTHORSHIP

Dispersal through the understorey: characterising genetic connectivity of the southern scrub-robin (*Drymodes burnneopygia*) in response to historical and contemporary landscapes

This chapter has been prepared as a submission for publication.

**Jolene Scoble**
Sought and won funding, designed and executed field sampling, completed all laboratory work and data analysis, and prepared manuscript as principle author.

Signed:
Date: 27/01/2012

**David Pavlacky**
Design of analysis framework, assistance with data analysis, commented on manuscript.

Signed:
Date: 21/01/2012

**Peter Cale**
Assisted with design and execution of field sampling.

Signed:
Date: 21/01/2012

**Michael George Gardner**
Provided guidance on, and assisted with laboratory work and data analysis, and commented on manuscript.

Signed:
Date: 24/01/2012

**Anita Smyth**
Assisted with design and execution of field sampling.

Signed:
Date: 19/01/2012
Andrew John Lowe
Assisted with design of field sampling, provided guidance on laboratory work and data analysis, and commented on manuscript.

Signed:
Date: 30/01/2012
Abstract

When animals disperse between habitat patches, the landscapes through which they choose to travel may be dissimilar in their composition, structure, resources and risks. Consequently different landscapes will have different levels of permeability to dispersal, with ramifications for microevolutionary processes such as gene flow and drift. Dispersal is therefore a critical aspect of population demography, an understanding of which is necessary for the judicious management of species for conservation. We investigated the effect of different landscape types on the dispersal patterns and population genetic structure of the southern scrub-robin (*Drymodes brunneopygia*), a ground dwelling avian species distributed across southern Australia. The southern scrub-robin is a species facing conservation challenges characteristics of many Australian species; a substantial amount of its range overlaps with land cleared and used for agriculture, while areas of its distribution under conservation may be at disproportionate threat from climate change.

We develop a set of *a priori* hypotheses seeking to explain the tendency of both historic and contemporary landscapes to facilitate or impede dispersal based on their structural attributes for the southern scrub-robin. This approach enabled us to elucidate the effect of both natural habitat heterogeneity as well as anthropogenic change on genetic structure, as well as the cumulative outcome of gene flow across generations. Multiple working hypotheses for both historic and contemporary environments were evaluated using information-theoretic model selection to avoid confounding the spatial and temporal aspects of dispersal. Patch density was the most important predictor of genetic connectivity in both historical (ΔAICₜₙ: 0.0; wᵢ: 0.080) and contemporary landscapes (ΔAICₜₙ: 0.1; wᵢ: 0.076). Landscape types with an open or inaccessible understorey were shown to increase population genetic structure in the southern scrub-robin, in particular chenopod habitat. Conversely, landscape types that offered a dense, accessible understorey structure decreased genetic structuring, possibly due to increased predator protection and foraging opportunities during dispersal. If climate change renders the large conservation parks which are now the mainstay of the southern scrub-robin unsuitable, restoration activities in agricultural areas seeking to maintain genetic diversity within the metapopulation should focus on understorey structure to enhance dispersal.
Introduction

The process of dispersal in animals has important consequences not only for individual fitness, but also for the abundance, distribution and genetic structure of a species. Dispersal is mediated by the habitat matrix, in which different landscape types may either facilitate or impede dispersal due to differential food availability, competition, predation risk, and shelter from climatic extremes (Ricketts 2001). Given the relationship between dispersal and population dynamics, understanding dispersal may be considered a fundamental aspect of managing species in the face of anthropogenic threats such as habitat fragmentation and climate change (Bowler and Benton 2005).

Many studies seeking to understand dispersal, particularly the impact of habitat loss, may confound their results by not properly considering the spatial and temporal aspects of dispersal (Keyghobadi 2007). Frequently dispersal studies seek to compare population structure in fragmented environment with a reference, intact environment (e.g. Broquet et al. 2006, Macqueen et al. 2008), disregarding the effect of natural habitat heterogeneity and potentially rendering comparisons with contemporary habitat loss futile (Pavlacky et al 2009). Furthermore, patterns of population genetic structure represent the cumulative outcome of gene flow from many generations past (Burel et al. 1998), such that the impact of habitat fragmentation may take many generations to become evident (Crow and Aoki 1984, Varvio et al. 1986, Holzhauer et al. 2006, Orsini et al. 2008). Contemporary patterns of gene flow may be best understood by characterising the relative contribution that both historic and contemporary landscapes have on landscape connectivity (Keyghobadi et al. 2005, Storfer et al. 2007, Pavlacky et al. 2009). The utility of dispersal studies may be further enhanced by analysis methods that move away from problematic Mantel tests (Raufaste and Rousset 2001, Castellano and Balletto 2002, Rousset 2002, Yang 2004, Balkenhol et al. 2009b) and the subjective costing of landscape types (e.g. least cost path analysis, Adriaensen et al. 2003), toward quantitatively estimating the effect of multiple environmental variables and interactions within a single population genetic model (Storfer et al. 2010).
One such landscape genetics approach, developed by Pavlacky et al. (2009), brings together existing analytical tools to characterise the spatial and temporal drivers of gene flow while circumventing the statistical and analytical drawbacks of alternative approaches. Initially, a linear mixed model is engaged to evaluate multiple a priori hypotheses predicting the effect of land cover on gene flow (Yang 2004, Selkoe et al. 2010). Alternative hypotheses are then evaluated using information-theoretic model selection (Burnham and Anderson 2001, 2002) to partition the respective effects of historic (pre-anthropogenic change) and contemporary landscapes on observed genetic connectivity and assess different land cover types for their ability to facilitate gene flow. Pavlacky et al.’s (2009) approach moves away from null hypothesis testing and limited inference from the binary application of statistical significance (Burnham and Anderson 2001). Furthermore, by considering multiple working hypotheses simultaneously (multi-model inference) (Burnham and Anderson 2001), the effects of predictive land cover variables can be averaged to reduce bias and imprecision associated with only considering the best model (Burnham and Anderson 1998).

We develop a set of a priori hypotheses regarding the impact of landscape types on gene flow for our study species, the southern scrub-robin (Drymodes branneopygia) (RAOU, 1926), a ground-dwelling bird species distributed across southern Australia. Following Pavlacky et al.’s (2009) approach outlined above, we seek to understand the contribution each of historic and contemporary landscapes to the population genetic structure (pairwise $F_{ST}$ estimates generated using neutral microsatellites) on the southern scrub-robin in eastern South Australia. In this region, the southern scrub-robin faces challenges characteristic of those encountered by many other species whose distributions coincide with agricultural or urban areas, the conservation needs of which may be better met with a comprehensive understanding of dispersal patterns. In eastern South Australia, it is the northern fringe of the southern scrub-robin’s distribution that has been afforded the highest level of protection under the reserve system (within the Riverland Biosphere Reserve), largely because the climate and soils are inappropriate for agriculture. This is part of systemic pattern evident in the Australian protected areas network, in which reserves were established in areas economicallyunviable for human activities rather than to meet the needs of biodiversity (Fuller et al. 2010). Protected areas established in regions whose
climate constitute the upper tolerance of a given species may no longer afford them protection as predicted increases in temperature and decreasing rainfall associated with anthropogenically-forced climate change eventuate (Hannah et al. 2007, Holper 2007, Dunlop 2008). Areas that may buffer species against an increasingly extreme climate are frequently dominated by human activity, fragmenting natural ecosystems. Such is the case for the southern scrub-robin. South of the Riverland Biosphere Reserve lies an agricultural region known as the Murray Mallee, in which vegetation remnancy is currently estimated at 20%. In the near future, large reserves at the periphery of a species distribution become climatically unsuitable and agricultural areas become the mainstay of species like the southern scrub-robin. Successful conservation efforts will rely heavily on maintaining dispersal amongst populations embedded within the agricultural matrix to maintain large effective population sizes and high genetic diversity crucial to population persistence. Understanding the effect of cleared agricultural areas on gene flow, and which landscape types facilitate dispersal to pursue appropriate habitat protection and restoration activities will enable judicious conservation.

The southern scrub-robin is an ideal candidate for early-intervention conservation actions. While the scrub-robin is listed as of least concern and exists in large numbers, populations are disappearing from fragments in agricultural matrices and the species has a decreasing area of occupancy (Garnett and Crowley 2000). Conservation actions for species like the southern scrub-robin are frequently delayed while population numbers are high, however conservation efforts are better placed to succeed when initiated before crises occur. Furthermore, population dynamics (including dispersal patterns) of sedentary ground dwelling species such as the southern scrub-robin are considered disproportionately threatened by habitat changes compared to those in birds with different life histories because such changes frequently occur first and most radically at the ground level (Reid and Fleming 1992, Ford et al. 2001).

The objectives of this study are twofold; initially we sought to understand the contribution of both historic (pre-clearing) and contemporary environments to contemporary population genetic structure. Within each timeframe, we additionally sought to characterise the influence of different landscape types on population genetic structure. We hypothesise that those landscape types with sparse
understorey structure will provide less protection from predation and climatic extremes as well as fewer foraging opportunities, impeding gene flow among sample locations.

**Materials and methods**

*Study species*

The southern scrub-robin is a medium-sized (21 – 42 g) ground dwelling bird species distributed throughout the semi-arid mallee region of southern Australia (Higgins and Peter 2002). While described as an omnivore, the majority of its diet consists of ants and other invertebrates (Higgins and Peter 2002). Southern scrub-robins have adopted a primarily sedentary lifestyle maintaining a home territory for the purposes of foraging and reproduction (Higgins and Peter 2002). Members of this species are only physically capable of short bursts of flight due to their short rounded wings, and are well adapted to their ground dwelling habit as evidenced by their long tarsus and tail (Higgins and Peter 2002). As a ground-dwelling species, dispersal success in the southern scrub-robin may be particularly susceptible to habitat clearing, as it cannot rely on flight based escape responses for predator avoidance (Lima 1993). The scrub-robin is heavily reliant on low shrubs for camouflage from mammalian and avian predators (Schodde 1981, Higgins and Peter 2002), and it decreases in abundance where grazing has diminished vegetative ground cover (Cale and Mladovan 2007).

*Sampling locations*

The study area occurs in the mallee region of eastern South Australia, across an ecotone between intact (Riverland Biosphere Reserve; longitude: 140.600, latitude: -33.600) and relictual (Murray Mallee; 140.200, -34.800) habitat within an agricultural matrix. Sampling locations were selected to ensure variation in the composition and configuration of landscapes between the sampling locations. Average distance between sampling locations was 94.65 km ± 47.37 km (range of distances: 7.82 km to 191.80 km). In the north of the study region lies a cluster of conservation parks known as the Riverland Biosphere Reserve that were commercially grazed until the 1990’s (clearing of vegetation to
create pasture was very limited). The region is comprised of approximately 900,000 hectares, and is managed by both government and non-for-profit agencies. We sampled the southern scrub-robin at five locations within the Riverland Biosphere Reserve (Figure 5.1). We sampled at a further five locations in the southern region of our study area, the Murray Mallee. The Murray Mallee comprises 1,836,000 hectares, of which 20% is currently remnant. Approximately 31% of native vegetation was cleared in the Murray Mallee by 1930, with intensive clearing occurring until the 1980s (Willoughby 2006).

Figure 5.1 Map of the study area showing the sampling locations (abbreviations) nested within the historical and contemporary landscapes of eastern South Australia. Vegetation types are broadly classified according to their understorey.
Assessing vegetation structure between populations

Vegetation structure for both the pre-European landscape (referred to as “historic” landscape) and contemporary landscape were derived from the National Vegetation Information System (NVIS) raster layer for extant vegetation (cell size 100 m x 100 m), provided by Australian Government Department of the Environment and Water Resources (DEWR 2006). Data for this raster layer was compiled from a variety of state based sources, and was collected on ground between 1997 and 2004. Pre-European vegetation was reconstructed through the use of interpolation and modelling techniques that employed mapping and information on the present types and extent of vegetation, as well as historical records and aerial photographs. Vegetation types were reclassified using ArcGIS v9.3.1 based on their understorey characteristics into six categories; shrubby, chenopod, hummock grasslands, tussock grasslands, woodlands (no significant understorey) and cleared (agricultural cropping) habitats.

Sample location centroids were calculated as the mean of Universal Transverse Mercator capture coordinates at each location. Euclidian distance was calculated as the distance in kilometres between each pair of sample location centroids. The vegetation structure between each pair of sampling sites was characterised from a Euclidean, five km-wide buffered pathway for both historic and contemporary vegetation structure. We chose a five km width for our pathways as a compromise between path overlap, covering as much of the study area as possible, and suitable sampling of the habitat likely encountered by dispersing scrub-robins over considerable distances. We then calculated the amount and percentage of each vegetation type and vegetation patch density within each pairwise pathway using the program FRAGSTATS, a program that calculates landscape metrics using categorical map patterns (McGarigal et al. 2002). Additionally, for the contemporary landscape, we calculated the amount and percentage of total vegetation in each buffer.

DNA sampling
A total of 173 southern scrub-robins were captured and sampled for DNA (between 11 and 22 per location, average 17) across the study area. Individual birds were trapped using a 9 m long, 38 mm mesh size mist-net with the aid of a territorial vocalisations broadcast from a small speaker adjacent to the mist-net. A 28 gauge needle was used to draw a small amount (~5µl) of blood from each bird. Blood was captured using Whatman’s® FTA elute cards and stored at room temperature with silica. DNA extraction was carried out in accordance with the procedure specified by Whatman®. The DNA was stored at -20 ºC.

We genotyped all 173 Drymodes brunneopygia sampled at 10 specific microsatellite loci following Scoble et al. (2011). Alleles were scored using the program GENEMAPPER® (version 3, Applied Biosystems) and checked manually. To calculate a genotyping error, we repeat-genotyped approximately 11% of samples for each marker, and calculated scoring errors per allele and per reaction for each locus and summarised across all loci (sensu Hoffman and Amos 2005).

Data analysis

Genotypes for each locus were tested for linkage disequilibrium (Lewontin and Kojima 1960) and departures from Hardy-Weinberg equilibrium (Guo and Thompson 1992) using ARLEQUIN 3.5.1.2 (Excoffier and Lischer 2010). The sequential Bonferroni procedure (Rice 1989) was applied to adjust significance levels (α = 0.05). We used Brookfield’s (1996) method to estimate the frequency of null alleles at each locus due to deviations from Hardy-Weinberg equilibrium (heterozygote deficiency), implemented within the program MICRO-CHECKER (Van Oosterhout et al. 2004). Micro-checker was also utilised to check for allele scoring errors due to stuttering and large allele drop out. Finally, ARLEQUIN was also used to calculate locus-specific $F_{IS}$ values, as further check for the presence of null alleles (null alleles are known to have a strong effect on genotype-based statistics such as $F_{IS}$).

Genetic diversity was measured for each location as observed ($H_o$) and expected ($H_e$) heterozygosity (Nei 1978), as well as the inbreeding coefficient $F_{IS}$ (Wier and Cockerham 1984) using ARLEQUIN. Additionally, allelic richness (AR) and the number of private alleles (PA) were calculated using a
rarefaction approach (Hurlbert 1971, Petit et al. 1998, Kalinowski 2004) in the program ADZE (Szpiech et al. 2008). The rarefaction method ensures the impact of unequal sample sizes on estimates is mediated by standardising all sample sizes so that each are equal to or less than the smallest sample size. The degree of genetic differentiation between sampling locations was estimated pairwise $F_{ST}$ measures (Wier and Cockerham 1984) using ARLEQUIN. The sequential Bonferroni procedure (Rice 1989) was applied to adjust significance levels ($\alpha = 0.05$).

We used the program 2MOD to investigate the migration-drift equilibrium of the metapopulation under study (Ciofi et al. 1999). Allelic history among sampling locations was assessed using 2MOD by comparing the likelihood of two competing models of demographic history; the gene flow model assumes differentiation is due to a balance between drift and immigration, while the drift model ascribes historical drift as the primary cause of genetic differentiation (Ciofi et al. 1999). We ran the 2MOD simulation for 100,000 iterations, discarding the first 10,000 as burn in before assessing the strength of evidence of competing models. Additionally we estimated the posterior distribution of $F$ for each sampling location, which characterises the contribution of immigration and drift on gene frequencies (Ciofi et al. 1999).

**Selecting a covariance structure**

Linearized pairwise $F_{ST}$ estimates were investigated as the dependent response variable to seven predictor vegetation variables characterised by understorey characteristics (shrubby, chenopod, hummock grasslands, tussock grasslands, woodlands and cleared habitats) between sampling locations, in addition to distance (km). Each predictor variable was used in univariate and in bivariate combinations, precluding those with a Spearman’s rank correlation coefficient ($r_s$) above 0.65. This gave us a candidate set of 25 models for the historic landscape and 39 models for the contemporary landscape (a substantially larger set due to the inclusion of total vegetation and cleared habitat). We hypothesised that the characteristics of each understorey type determine available predator protection,
Table 5.1 Predictor vegetation variables and their hypothesised relationship with southern scrub-robin survival during dispersal and population genetic structure, as measured by \((F_{ST}/(1 - F_{ST}))\).

<table>
<thead>
<tr>
<th>Habitat metric</th>
<th>Predator protection</th>
<th>Food availability</th>
<th>Other factors</th>
<th>Hypothesised relationship to population genetic structure ((F_{ST}/(1 - F_{ST})))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chenopod</td>
<td>Comparatively open habitat may facilitate higher predation rate</td>
<td>Vegetation structural diversity low, decreasing invertebrate abundance and diversity</td>
<td>Lack of overstorey may increase exposure to inclement weather</td>
<td>+ve</td>
</tr>
<tr>
<td>Shrubby</td>
<td>High visual and structural protection by shrubby understory</td>
<td>Habitat heterogeneity and comparatively high moisture levels facilitate excellent foraging opportunities</td>
<td>Intraspecific competition may limit dispersal</td>
<td>-ve</td>
</tr>
<tr>
<td>Tussock</td>
<td>Moderate level of visual protection offered by grassy understory</td>
<td>Habitat heterogeneity provides good foraging opportunities</td>
<td>Not applicable</td>
<td>-ve</td>
</tr>
<tr>
<td>Hummock</td>
<td>Low, scrub-robins unable to seek shelter under hummock grass</td>
<td>Habitat heterogeneity provides good foraging opportunities</td>
<td>Highly flammable habitat type</td>
<td>+ve</td>
</tr>
<tr>
<td>Woodlands</td>
<td>Low, lack of understorey means scrub-robins are easier for predators to see</td>
<td>Habitat heterogeneity provides good foraging opportunities</td>
<td>Lack of understorey may increase exposure to inclement weather</td>
<td>+ve</td>
</tr>
<tr>
<td>Cleared</td>
<td>Very low, open habitat and high levels of predators such as foxes in agricultural habitats</td>
<td>Decreased diversity and abundance of potential food sources</td>
<td>Lack of vegetation structure may increase exposure to inclement weather</td>
<td>+ve</td>
</tr>
<tr>
<td>Total vegetation(^1)</td>
<td>Increased predator protection compared to cleared habitats</td>
<td>Increased food availability compared to cleared habitats</td>
<td>Not applicable</td>
<td>-ve</td>
</tr>
<tr>
<td>Patch density(^2)</td>
<td>Not applicable</td>
<td>Not applicable</td>
<td>Increasing spatial heterogeneity decreases likelihood of dispersal</td>
<td>+ve</td>
</tr>
<tr>
<td>Distance</td>
<td>Longer distances increases chance of encountering predator</td>
<td>Longer distances increases chance of starvation</td>
<td>Isolation by distance effects</td>
<td>+ve</td>
</tr>
</tbody>
</table>

1. Total vegetation was calculated for the contemporary landscape as the percentage of each buffer that was comprised of native vegetation (total area of buffer – area of cleared land * 100)
2. Patch density (PD) was calculated as: \(PD = n/A (10,000 \times 100)\) where \(n_i\) = number of patches in the landscape of patch type (class) \(i\), and \(A = \) total landscape area (m\(^2\)) multiplied by 10,000 and 100 (to convert to 100 hectares).
food, and other factors for the dispersing southern scrub-robin. These resources and risks influence dispersal decisions and success, and hence genetic structuring among sample locations (Table 5.1).

Because pairwise $F_{ST}$ estimates incorporate multiple instances of the same population, the estimates are not independent. We therefore employed a linear mixed model to account for the non-independence of estimates, and to understand the effect of distance and vegetation understory on genetic structure. To evaluate the ability of four different covariance structures to explain genetic structure as measured by $[F_{ST}/(1 - F_{ST})]$ (Rousset 1997), we employed the restricted maximum likelihood approach in SAS PROC MIXED (SAS Institute 1999). The residuals of genetic structure $[F_{ST}/(1 - F_{ST})]$ were calculated for independent observations using variance component (VC) model, and dependent observations using three different models to estimate autocorrelation amongst residuals. First-order autoregressive [AR(1)] and first-order autoregressive moving-average [ARMA(1,1)] covariance models characterised the relationship of residuals with distance, specified by the covariance parameter rho (Yang 2004). The Toeplitz [TOEP(1)] covariance structure additionally treats multiple instances of the locations as random effects with a banded, autoregressive moving-average structure (Selkoe et al. 2010). The most appropriate covariance structure was selected based upon AICc values and the subsequent calculation of likelihood-ratio tests for competing models.

Assessing competing models

Information-theoretic model selection (Burnham and Anderson 2001, 2002) was employed to assess univariate and bivariate models representing different competing hypotheses seeking to explain genetic structure. We equalised the number of historic and contemporary models within a single assessment framework. Models were ordered according to their Akaike’s (1992) information criterion corrected for small sample size ($AIC_c$), and then ranked based upon their $\Delta AIC_c$. We calculated model $AIC_c$ weights ($w_i$) to assess the support for individual models and employed the weights to calculate evidence ratios to compare the strength of evidence for individual models. For example, the evidence ratio for model A and model B is the ratio of the individual $AIC_c$ weights for each model $[w_{modelA}/w_{modelB}]$. For both historic and contemporary time frames we summed the model weights $[w_e(j)]$ in
order to derive an evidence ratio \( w_{\text{contemporary}}(j) / w_{\text{historic}}(j) \) of the relative contribution of each landscape to observed genetic structure. Models with a \( \Delta \text{AIC}_c < 4 \) within each time frame were employed in the calculation of model averaged parameter estimates (\( \beta \)), unconditional standard errors (SE) and 95% confidence intervals (CI), as well as coefficients of variation (CV). We chose a cut off value of \( \Delta \text{AIC}_c < 4 \) as this represents a conservative group of plausible hypotheses (Figure 2; Symonds and Moussalli 2011).

**Results**

*Vegetation between sampling locations*

In the historic landscape, vegetation was dominated by tussock grass and shrubby understorey types (Table 5.2). In the contemporary landscape, almost half of the vegetation that existed between sampling locations has been cleared, including substantial losses of tussock grass and chenopod. Shrubby understorey types dominate the contemporary landscape.

**Table 5.2 Amount (in hectares) and the percentage representation of different vegetation types.**
Vegetation type is classified by understorey prior to anthropogenic change (historic) and in the current landscape (contemporary) within buffered pathways. Data derived from National Vegetation Information System (cell size 100 m x 100 m), provided by Australian Government Department of the Environment and Water Resources (DEWR 2006).

<table>
<thead>
<tr>
<th>Habitat metric</th>
<th>Historic</th>
<th>Contemporary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chenopod</td>
<td>92,894 (7%)</td>
<td>21,796 (2%)</td>
</tr>
<tr>
<td>Shrubby</td>
<td>439,576 (34%)</td>
<td>439,772 (33%)</td>
</tr>
<tr>
<td>Tussock</td>
<td>550,808 (42%)</td>
<td>47,344 (4%)</td>
</tr>
<tr>
<td>Hummock</td>
<td>195,675 (15%)</td>
<td>191,009 (15%)</td>
</tr>
<tr>
<td>Woodlands</td>
<td>29,953 (2%)</td>
<td>29,953 (2%)</td>
</tr>
<tr>
<td>Cleared</td>
<td>n/a</td>
<td>578,967 (44%)</td>
</tr>
<tr>
<td>Total vegetation</td>
<td>1,308,909 (100%)</td>
<td>729,876 (56%)</td>
</tr>
</tbody>
</table>
Assessing loci

Regenotyping of samples revealed scoring errors for loci DRYB29 and DRYB34, representing an error rate of 0.0313 per reaction, or 0.0156 per allele for each locus. Summarised across all loci, this equates to an error rate per reaction of 0.0071 and 0.0035 per allele. We found no evidence of scoring errors due to large allele drop-out or stuttering. We did however detect deviations from Hardy-Weinberg equilibrium at four loci (DRYB15, DRYB21, DRYB29, DRYB34) using both MICROCHECKER and ARLEQUIN. Deviations from Hardy-Weinberg equilibrium can be due to subpopulation structure (Wahlund effect), inbreeding, or the presences of null (non-amplified) alleles. Significant deviations from Hardy-Weinberg equilibrium for loci DRYB12, DRYB29 and DRYB34 were only detected for two populations using MICROCHECKER, and for one population using ARLEQUIN. Locus DRYB21 had evidence of null alleles at four populations using MICROCHECKER and one population using ARLEQUIN. We calculated $F_{IS}$ for each locus, as the presence of null alleles is known to have a strong effect on genotype-based statistics such as $F_{IS}$. We found that locus DRYB21 had an $F_{IS}$ value of more than double that of any other locus. On the basis of these combined results, we decided that loci DRYB12, DRYB29 and DRYB34 were most likely experiencing deviations from Hardy-Weinberg equilibrium due to population-specific genetic processes. As locus DRYB21 had both evidence of deviations from Hardy-Weinberg equilibrium and a relatively high $F_{IS}$ value, it was dropped from further analysis due to the probable presence of null alleles. Linkage disequilibrium was also detected for 5 locus pairs, comprising just 0.82% of total pairs assessed (36 locus comparisons for each of 17 populations). Because no one pair of loci was found to be in linkage disequilibrium more than once, and the very low level of linkage disequilibrium in total, we also attributed this result to population-specific genetic processes.

Observed genetic structure and diversity

Sampling locations located in the agricultural matrix have the highest levels of genetic diversity (Table 5.3). Billiatt CP South and North, southern-most in the Murray Mallee’s agricultural matrix, both had
Table 5.3 Locations (and their abbreviations) of sampled southern scrub-robins and calculated genetic indices. We report the number of southern scrub-robins sampled per location, probability that two genes share a common ancestor (F) as well as lower (LCI) and upper (UCI) 95% confidence intervals for F, observed ($Ho$) and expected ($He$) heterozygosities, fixation index ($F_{IS}$), allelic richness ($AR$) and private alleles ($PA$). Allelic richness and private alleles values were rarefied to 11 individuals per location.

<table>
<thead>
<tr>
<th>Location</th>
<th>Abbreviation</th>
<th>N</th>
<th>F</th>
<th>LCI</th>
<th>UPI</th>
<th>$Ho$</th>
<th>$He$</th>
<th>$F_{IS}$</th>
<th>$AR$†</th>
<th>$PA$†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yookamurra Sanctuary</td>
<td>YM</td>
<td>18</td>
<td>0.039</td>
<td>0.024</td>
<td>0.083</td>
<td>0.618</td>
<td>0.690</td>
<td>0.087</td>
<td>3.943</td>
<td>0.115</td>
</tr>
<tr>
<td>Brookfield CP</td>
<td>BR</td>
<td>11</td>
<td>0.102</td>
<td>0.051</td>
<td>0.173</td>
<td>0.545</td>
<td>0.671</td>
<td>0.195</td>
<td>3.749</td>
<td>0.072</td>
</tr>
<tr>
<td>Henry's Block</td>
<td>HB</td>
<td>18</td>
<td>0.052</td>
<td>0.026</td>
<td>0.105</td>
<td>0.569</td>
<td>0.673</td>
<td>0.146</td>
<td>3.660</td>
<td>0.070</td>
</tr>
<tr>
<td>Froggy Dam</td>
<td>FD</td>
<td>17</td>
<td>0.034</td>
<td>0.017</td>
<td>0.069</td>
<td>0.660</td>
<td>0.704</td>
<td>0.064</td>
<td>3.956</td>
<td>0.024</td>
</tr>
<tr>
<td>Long Dam</td>
<td>LD</td>
<td>18</td>
<td>0.047</td>
<td>0.025</td>
<td>0.094</td>
<td>0.630</td>
<td>0.690</td>
<td>0.090</td>
<td>3.850</td>
<td>0.043</td>
</tr>
<tr>
<td>Taylorville Station</td>
<td>TS</td>
<td>16</td>
<td>0.061</td>
<td>0.035</td>
<td>0.108</td>
<td>0.632</td>
<td>0.709</td>
<td>0.112</td>
<td>3.945</td>
<td>0.073</td>
</tr>
<tr>
<td>Hideaway Block</td>
<td>HD</td>
<td>18</td>
<td>0.030</td>
<td>0.011</td>
<td>0.069</td>
<td>0.668</td>
<td>0.700</td>
<td>0.034</td>
<td>3.938</td>
<td>0.009</td>
</tr>
<tr>
<td>BilliattCP South</td>
<td>BS</td>
<td>22</td>
<td>0.002</td>
<td>0.000</td>
<td>0.013</td>
<td>0.662</td>
<td>0.728</td>
<td>0.094</td>
<td>4.297</td>
<td>0.153</td>
</tr>
<tr>
<td>BilliattCP North</td>
<td>BN</td>
<td>16</td>
<td>0.006</td>
<td>0.001</td>
<td>0.029</td>
<td>0.736</td>
<td>0.717</td>
<td>-0.027</td>
<td>4.156</td>
<td>0.052</td>
</tr>
<tr>
<td>Dangalli CP</td>
<td>DG</td>
<td>19</td>
<td>0.042</td>
<td>0.022</td>
<td>0.083</td>
<td>0.690</td>
<td>0.674</td>
<td>-0.025</td>
<td>3.820</td>
<td>0.011</td>
</tr>
</tbody>
</table>
Table 5.4. Pairwise population differentiation ($F_{ST}$) for pairs of southern scrub-robin populations in eastern South Australia. Estimates of pairwise $F_{ST}$ that are significant ($P < 0.05$) after applying the sequential Bonferroni correction are underlined.

<table>
<thead>
<tr>
<th></th>
<th>YM</th>
<th>BR</th>
<th>HB</th>
<th>FD</th>
<th>LD</th>
<th>TS</th>
<th>HD</th>
<th>BS</th>
<th>BN</th>
<th>DG</th>
</tr>
</thead>
<tbody>
<tr>
<td>YM</td>
<td>—</td>
<td>0.075</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BR</td>
<td></td>
<td>0.051</td>
<td>0.052</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HB</td>
<td>0.040</td>
<td>0.076</td>
<td>0.053</td>
<td>0.035</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FD</td>
<td></td>
<td>0.028</td>
<td>0.080</td>
<td>0.058</td>
<td>0.035</td>
<td>0.048</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LD</td>
<td>0.026</td>
<td>0.048</td>
<td>0.028</td>
<td>0.017</td>
<td>0.030</td>
<td>0.020</td>
<td>—</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TS</td>
<td></td>
<td>0.020</td>
<td>0.055</td>
<td>0.012</td>
<td>0.023</td>
<td>0.024</td>
<td>0.029</td>
<td>0.007</td>
<td>—</td>
<td></td>
</tr>
<tr>
<td>HD</td>
<td></td>
<td>0.032</td>
<td>0.051</td>
<td>0.001</td>
<td>0.023</td>
<td>0.030</td>
<td>0.030</td>
<td>0.028</td>
<td>-0.001</td>
<td>—</td>
</tr>
<tr>
<td>BS</td>
<td>0.067</td>
<td>0.070</td>
<td>0.013</td>
<td>0.031</td>
<td>0.045</td>
<td>0.045</td>
<td>0.025</td>
<td>0.022</td>
<td>0.008</td>
<td>—</td>
</tr>
</tbody>
</table>

the highest levels of $H_e$ (BS: 0.728, BN: 0.717) and $AR$ (BS: 4.297, BN: 4.156). Two sampling locations in the agricultural matrix also had the highest values of $PA$, Yookamurra Sanctuary (0.115) and Billiatt CP South (0.153). The highest levels of inbreeding were likewise found in the agricultural matrix (average $F_{IS}$; agricultural matrix 0.099, contiguous vegetation 0.055), in particular Brookfield CP (0.195) and Henry’s Block (0.146) but high levels were also present in contiguous habitat ($F_{IS}$; TS 0.112). Genetic structure as measured by pairwise $F_{ST}$ estimates suggests only a small level of structuring within the study area (Table 5.4). The average pairwise $F_{ST}$ estimate is only 0.037. The highest pairwise estimate occurs across the ecotone between the Riverland Biosphere Reserve, and the Murray Mallee, between Yookamurra Sanctuary and Long Dam ($F_{ST} = 0.081$). The lowest pairwise $F_{ST}$ estimate originates within Billiatt Conservation Park, between the north and south sampling locations ($F_{ST} = -0.001$), and indicates virtually no structuring within this large remnant.

Analysis of migration-drift equilibrium using 2MOD indicates that the non-equilibrium drift model is marginally better at explaining population structure than the equilibrium migration-
drift model (posterior probability = 0.5323, SE = 0.0037), with a Bayes factor of 1.138. Most populations had a trend of moderate to high levels of genetic drift (0.030 ≤ F ≤ 0.102), although in Billiatt CP, immigration was clearly the most important source of genetic structure (BS; \( F = 0.002, \text{CI 0.001, 0.013} \), BN; \( F = 0.006, \text{CI 0.001, 0.029} \)).

**Covariance structure and competing models explaining genetic structure**

Residual error for pairwise \( \frac{F_{ST}}{1 - F_{ST}} \) estimates was best explained by the TOEP (1) covariance structure using the restricted maximum likelihood framework in SAS (\( \chi^2 = 11.1, P < 0.001 \)). Therefore we employed the TOEP (1) covariance structure in our subsequent assessment of competing historic and contemporary landscape structure models.

The effect of different landscape covariates on genetic structure was consistent with our predictions. Patch density, chenopod, hummock grasslands, woodlands, cleared areas and distance all increased genetic structure (Table 5.5). Likewise, shrubby and tussock grass understorey habitat types, as well as total vegetation (contemporary landscape only) decreased genetic structure. However, many of the effect sizes are weak, as indicated by 95% confidence limits that cover zero (Table 5.6). Habitat models drawn from the contemporary landscape accounted for approximately 60% \( \left[ w_i(j) = 0.587 \right] \) of model weights, 1.5 times that of the historic landscape \( \left[ w_i(j) = 0.386 \right] \). However the best model was drawn from the historic time frame, wherein patch density (\( \text{km}^{-2} \)) increaesd genetic structure (Table 5.5, Figure 5.2). In fact patch density featured in all the top historic models bar the univariate chenopod model, ranked fourth. The univariate patch density model has a weight 3.5 times that of the chenopod model. Despite a small reduction in patch density over time (Figure 5.2), the best model for the contemporary habitat was also patch density, establishing the effect of increasing genetic structure (Table 5.5, Figure5.2). However its weight was just 1.1 times that
### Table 5.5 Models of historic and contemporary landscape structure weighted by their effect on pairwise population differentiation ($F_{ST}/(1-F_{ST})$) for the southern scrub-robin in South Australia.

Landscape metrics within each model indicate the direction of influence (+ or -) on $F_{ST}/(1-F_{ST})$. Statistics presented include number of parameters ($K$), log likelihood, Akaike’s information criterion corrected ($AIC_c$), difference between smallest (best model) and model $AIC_c$, and $AIC_c$ weights ($w_i$). Only models with a $\Delta AIC_c \leq 2.5$ are displayed.

<table>
<thead>
<tr>
<th>Time period</th>
<th>$\beta_1$</th>
<th>$\beta_2$</th>
<th>$K$</th>
<th>Log(L)</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Historic</td>
<td>+Patch density</td>
<td>+Patch density</td>
<td>4</td>
<td>124.1</td>
<td>-239.2</td>
<td>0.0</td>
<td>0.080</td>
</tr>
<tr>
<td></td>
<td>+Distance</td>
<td>+Patch density</td>
<td>5</td>
<td>124.45</td>
<td>-237.4</td>
<td>1.8</td>
<td>0.032</td>
</tr>
<tr>
<td></td>
<td>-Tussock grass</td>
<td>+Patch density</td>
<td>5</td>
<td>124.35</td>
<td>-237.2</td>
<td>2</td>
<td>0.029</td>
</tr>
<tr>
<td></td>
<td>+Log$_e$ chenopod</td>
<td>+Patch density</td>
<td>4</td>
<td>122.85</td>
<td>-236.7</td>
<td>2.5</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td>-Shrubby</td>
<td>+Patch density</td>
<td>5</td>
<td>124.1</td>
<td>-236.7</td>
<td>2.5</td>
<td>0.023</td>
</tr>
<tr>
<td></td>
<td>+Woodland</td>
<td>+Patch density</td>
<td>5</td>
<td>124.1</td>
<td>-236.7</td>
<td>2.5</td>
<td>0.023</td>
</tr>
<tr>
<td>Contemporary</td>
<td>+Patch density</td>
<td>+Patch density</td>
<td>4</td>
<td>124.05</td>
<td>-239.1</td>
<td>0.1</td>
<td>0.076</td>
</tr>
<tr>
<td></td>
<td>+Log$_e$ chenopod</td>
<td>+Patch density</td>
<td>4</td>
<td>123.95</td>
<td>-238.9</td>
<td>0.3</td>
<td>0.069</td>
</tr>
<tr>
<td></td>
<td>+Log$_e$ chenopod</td>
<td>+Patch density</td>
<td>5</td>
<td>125</td>
<td>-238.5</td>
<td>0.7</td>
<td>0.056</td>
</tr>
<tr>
<td></td>
<td>+Distance</td>
<td>+Patch density</td>
<td>5</td>
<td>124.3</td>
<td>-237.1</td>
<td>2.1</td>
<td>0.028</td>
</tr>
<tr>
<td></td>
<td>+Log$_e$ cleared</td>
<td>+Patch density</td>
<td>4</td>
<td>123</td>
<td>-237</td>
<td>2.2</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>+Log$_e$ chenopod</td>
<td>+Log$_e$ hummock grass</td>
<td>5</td>
<td>124.2</td>
<td>-236.9</td>
<td>2.3</td>
<td>0.025</td>
</tr>
<tr>
<td></td>
<td>-Tussock grass</td>
<td>+Patch density</td>
<td>5</td>
<td>124.25</td>
<td>-236.9</td>
<td>2.3</td>
<td>0.025</td>
</tr>
<tr>
<td>Distance</td>
<td>+Distance</td>
<td>+Patch density</td>
<td>4</td>
<td>123</td>
<td>-237</td>
<td>2.2</td>
<td>0.027</td>
</tr>
</tbody>
</table>
Table 5.6 Model averaged parameters of each habitat metric for both historic and contemporary landscapes. Habitat metrics are ranked by their Coefficient of Variation (CV). Statistics presented are the Estimate ($\beta$), Standard Error, 95% Lower (LCL) and Upper Confidence Limits (UCL) and Coefficient of Variation (CV).

<table>
<thead>
<tr>
<th>Time period</th>
<th>Habitat metric</th>
<th>Estimate ($\beta$)</th>
<th>Standard error</th>
<th>LCL</th>
<th>UCL</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>Historic</td>
<td>patch density</td>
<td>0.04685</td>
<td>0.02376</td>
<td>0.00027</td>
<td>0.09342</td>
<td>0.507</td>
</tr>
<tr>
<td></td>
<td>chenopod</td>
<td>0.00491</td>
<td>0.00299</td>
<td>-0.00095</td>
<td>0.01077</td>
<td>0.609</td>
</tr>
<tr>
<td></td>
<td>hummock</td>
<td>0.00352</td>
<td>0.00313</td>
<td>-0.00261</td>
<td>0.00965</td>
<td>0.889</td>
</tr>
<tr>
<td></td>
<td>distance</td>
<td>0.000005</td>
<td>0.00005</td>
<td>-0.00004</td>
<td>0.00014</td>
<td>0.934</td>
</tr>
<tr>
<td></td>
<td>shrubby</td>
<td>-0.00008</td>
<td>0.00015</td>
<td>-0.00037</td>
<td>0.00021</td>
<td>1.818</td>
</tr>
<tr>
<td></td>
<td>tussock</td>
<td>-0.00006</td>
<td>0.00016</td>
<td>-0.00037</td>
<td>0.00025</td>
<td>2.605</td>
</tr>
<tr>
<td></td>
<td>woodlands</td>
<td>0.00017</td>
<td>0.00055</td>
<td>-0.00090</td>
<td>0.00125</td>
<td>3.189</td>
</tr>
<tr>
<td>Contemporary</td>
<td>chenopod</td>
<td>0.00748</td>
<td>0.00401</td>
<td>-0.00038</td>
<td>0.01533</td>
<td>0.536</td>
</tr>
<tr>
<td></td>
<td>patch density</td>
<td>0.04542</td>
<td>0.02551</td>
<td>-0.00457</td>
<td>0.09542</td>
<td>0.562</td>
</tr>
<tr>
<td></td>
<td>hummock</td>
<td>0.00286</td>
<td>0.00320</td>
<td>-0.00340</td>
<td>0.00913</td>
<td>1.117</td>
</tr>
<tr>
<td></td>
<td>distance</td>
<td>0.000004</td>
<td>0.00005</td>
<td>-0.00006</td>
<td>0.00014</td>
<td>1.237</td>
</tr>
<tr>
<td></td>
<td>cleared</td>
<td>0.00152</td>
<td>0.00201</td>
<td>-0.00241</td>
<td>0.00545</td>
<td>1.323</td>
</tr>
<tr>
<td></td>
<td>tussock</td>
<td>-0.00021</td>
<td>0.00035</td>
<td>-0.00088</td>
<td>0.00047</td>
<td>1.665</td>
</tr>
<tr>
<td></td>
<td>shrubby</td>
<td>-0.00007</td>
<td>0.00015</td>
<td>-0.00036</td>
<td>0.00022</td>
<td>2.043</td>
</tr>
<tr>
<td></td>
<td>total vegetation</td>
<td>-0.00003</td>
<td>0.00007</td>
<td>-0.00018</td>
<td>0.00011</td>
<td>2.200</td>
</tr>
<tr>
<td></td>
<td>woodlands</td>
<td>0.00005</td>
<td>0.00046</td>
<td>-0.00084</td>
<td>0.00094</td>
<td>9.136</td>
</tr>
</tbody>
</table>
Figure 5.2. Relationship between \( F_{ST}/(1 - F_{ST}) \) and the top two habitat metrics (as measured by AIC\(_c\) weights \((w_i)\)) for both historic (patch density; A.1 and distance; A.2) and contemporary (patch density; B.1 and chenopod; B.2) landscapes. Trend lines and 95% confidence limits are compiled from model averaged values drawn from models with a \( \Delta \text{AIC}_c \leq 4 \).
of the univariate chenopod model (Table 5.5, figure 5.2). The univariate model for cleared areas had the effect of increasing $[F_{ST}/(1 - F_{ST})]$ estimates, but this model was 2.8 times less probable than the top model containing patch density on the basis of AICc weights ($w_i$).

The model averaged effect of patch density in the historic landscape has the largest effect size (CV = 0.507) (Table 5.6). Both chenopod (CV = 0.609) and hummock grasslands (CV = 0.889) have a larger effect size than distance (CV = 0.934). Of the four top landscape metrics, only the effect of patch density on genetic structure has confidence intervals that avoid covering zero ($\hat{\beta} = 0.0469$, SE = 0.0238, CI = 0.0002, 0.0935), which indicates a large effect size for this variable. The effect of chenopod only narrowly covers zero ($\hat{\beta} = 0.0049$, SE = 0.0030, CI = -0.0010, 0.0108), which indicates a moderate effect size for this variable. In the contemporary landscape, the model averaged effect of patch density (CV = 0.562) has been superseded by that of chenopod (CV = 0.536), which has the largest effect size. The confidence intervals for the effect of chenopod narrowly cover zero ($\hat{\beta} = 0.0075$, SE = 0.0040, CI = -0.0004, 0.0154), indicating a moderate effect size. The model averaged effect of cleared land (CV = 1.323) is more than two times smaller than that of chenopod and only comes in as the fifth most important landscape metric.

**Discussion**

Never more so has it been important to understand dispersal characteristics of flora and fauna as it now. While habitat loss decreases the ability of many species to maintain dispersal networks and gene flow, climate change necessitates adaption or range shifts for many species. The southern scrub-robin is a species of low mobility whose natural range is fragmented by agriculture and is at threat from climate change in the protected area mainstays of its distribution. We have utilised a suite of novel statistical approaches, better able to accommodate complex, biologically realistic hypotheses of gene flow across a dynamic landscape, than other popular landscape genetic methods to understand dispersal in this species (Pavlacky et al. 2009). Multiple working hypotheses were derived from an empirically-based ecological model that considered factors influencing dispersal success in the
southern scrub-robin through different landscape types. We employed 5km wide buffers to capture the majority of potential dispersal routes between sampling locations. Competing hypotheses were then assessed using linear mixed models to estimate appropriate sampling variance and better account for non-independent pairwise ($F_{ST}$) data (Wolfinger 1993, Yang 2004). Multimodel inference (Burnham and Anderson 2001) enabled contemporary patterns of genetic structure to be partitioned into processes attributed to either the historical or contemporary landscapes, elucidating the effect of anthropogenic activity on dispersal. Furthermore, the effect of different landscape types within each time period could be evaluated for their relative permeability to gene flow.

Our prediction that understorey types providing comparatively less structure (including agricultural areas) would inhibit gene flow and increase genetic structure were confirmed. These landscapes are expected to offer decreased amounts and diversity of food (particularly invertebrate prey), increase exposure to weather and perhaps most importantly, predation. Understorey types that did offer accessible structural and/or visual protection from predators (e.g. shrubby understory) reduced genetic structure. This result is consistent with other empirical studies of ground-dwelling birds, which demonstrated reluctance to move through habitats that lack, or have a sparse understory (Sieving et al. 1996, Reid et al. 2004, Vergara and Simonetti 2006, Tomasevic and Estades 2008, Pavlacky et al. 2009). Avian species with poor flight ability, such as the southern scrub-robin, are unable to utilise high flight speed or aerial acrobatics to escape aerial predators. They therefore rely heavily on the presence of escape cover to facilitate predator avoidance (Lima 1993, Reid et al. 2004), and in its absence may succumb to higher levels of predation.

*Historic landscape*

Within our study area the observed population genetic structure is explained marginally better by a model of historic population divergence due to drift when compared with the likelihood of a model based on migration-drift equilibrium. However there is only a small difference in the likelihoods of the competing models. Furthermore, a bayes factor of less than three is not considered substantial support for one model over another (Kass and Raftery 1995), justifying an analysis of the impact of landscape
covariates on gene flow for the southern scrub-robin. While we are confident that our model selection approach is robust to the potential absence of migration-drift equilibrium, it will be unable to estimate an effect that doesn't yet have a signature in the genetic structure of the southern scrub-robin.

To understand the population genetic processes associated with anthropogenic landscape change, it is imperative that the effect of both contemporary and historic landscapes on gene flow is considered. While the effect of historic landscapes (Keyghobadi et al. 2005, Holzhauer et al. 2006, Pavlacky et al. 2009) and demography (Orsini et al. 2008) often prove to have an important legacy on contemporary genetic structure they are infrequently investigated (Storfer et al. 2010). Our results demonstrate the important effect historic, natural habitat heterogeneity continues to have on contemporary genetic structure in the southern scrub-robin.

In the historic landscape, spatial variation in habitat quality was the most important determinant of population genetic structure, acting to impede gene flow. Individuals in habitat patches of comparatively lower quality are expected to experience stronger motivation for dispersing to increase future fitness (Gadgil 1971, Hastings 1983, Greenwood-Lee and Taylor 2001). However given that lower quality habitats are also expected to contain fewer individuals, dispersal events are assumed to be uncommon (Bowler and Benton 2005). Furthermore, increasing spatial heterogeneity means dispersing individuals have an increased likelihood of encountering good quality habitat sooner, decreasing average dispersal distance (Levin et al. 1984, Hovestadt et al. 2001, Muller-Landau et al. 2003, Lowe 2009) and increasing population structuring.

The most important habitat type in the historic landscape was chenopod, which impeded gene flow in the southern scrub-robin. Chenopod habitat is characterised by a low, open structure, decreasing both predator cover and foraging opportunities. Critically, ant populations, which form a large part of the southern scrub-robins diet in South Australia (Higgins and Peter 2002), are less abundant in structurally depauperate habitats within the arid zone (Andersen 1983, Dangerfield et al. 2003). Hummock grasslands also greatly reduced gene flow in the historic habitat. Hummock grass species (e.g. *Triodia scariosa*) in eastern South Australia are typified by spikey, stiff blades that form a
hummock (Rice and Westoby 1999), which is impenetrable to the southern scrub-robin and hence provide no predator protection. Additionally, the highly flammable nature of hummock grasses (Rice and Westoby 1999, Nicholas et al. 2009) potentially disturbs dispersal events both directly and subsequently through the effects of decreased vegetative cover. A shrubby understorey, preferred habitat type of this species, was shown to weakly facilitate gene flow. Conspecifics holding territories in shrubby habitat through which a dispersing scrub-robin hopes to pass may exhibit aggression, and when occurring in high densities may constitute a social fence (Hestbeck 1982, Matthysen 2005, Pavlacky et al. 2009). Alternatively, dispersal may cease if appropriate shrubby habitat is encountered and a suitable territory may be established or won.

Contemporary landscape

In the contemporary landscape we find that the directionality and evidence ratios of most habitat metrics remains unchanged. We hypothesised that land clearing and introduced predators (primarily the fox) represent the chief novel threats to the success of dispersal for the southern scrub-robin. While cleared habitat did increase genetic structure, it ranked as only the fifth most important landscape metric after model averaging. Vegetation remnancy is relatively high in the Murray Mallee, at around 20% (Willoughby 2006). Furthermore, our sampling sites within the agricultural matrix were predominately located in remnant vegetation proximate to, and connected with, larger tracts of native vegetation. This pattern suggests that while southern scrub-robins sampled within the Murray Mallee occur within remnant habitat, it is neither highly fragmented nor isolating. Well-connected remnant habitat patches may facilitate high levels of gene flow evident between regions and counter the effects of reduced local population size and genetic drift affected by habitat loss (Keyghobadi et al. 2005). Supporting this conclusion is patch density, which was slightly lower in the contemporary landscape. A high level of habitat fragmentation would be expected to substantially increase patch density in the contemporary landscape. This result indicates that contemporary landscape patterns resulted from habitat loss rather than substantial habitat fragmentation.
A time lag between landscape change and its effects on observed genetic structure may also be responsible for the weak effect of cleared land reported on gene flow in the southern scrub-robin. If the system is not at migration-drift equilibrium, the effect of land clearing that was found in this study may become stronger in the future. Population genetic structure represents the cumulative outcome of gene flow from many generations past (Burel et al. 1998), such that the impact of habitat fragmentation may take many generations to become evident (Crow and Aoki 1984, Varvio et al. 1986, Holzhauer et al. 2006, Orsini et al. 2008). We report that the historic landscape is still responsible for approximately 40% of observed contemporary population genetic structure in the southern scrub-robin. This indicates that the effect of anthropogenic landscape change is far from fully expressed in the genetic signature of this species.

Clearing of native habitat for agriculture is known to act in synergy with other threats, including introduced predators. Fox densities occur at their highest in mixed agricultural landscapes, where a range of domestic, introduced and native prey items are also likely to be in high abundances (Pita et al. 2009, Arthur et al. 2010). We therefore expect that foxes might have the strongest impact on dispersal success in those habitat types that are not only lacking in visual and structural predator protection, but also are proximate to agricultural clearing. This is the case for chenopod habitat. Despite substantial clearing of chenopod habitat, it has become the most important habitat metric in the contemporary landscape, and may represent a strong barrier between locations in the Riverland Biosphere Reserve and locations YM and BR in the agricultural matrix. Fox predation is a particularly important cause of decline in ground-dwelling birds, such as the southern scrub-robin, as they are nest, feed and move along the ground, and lack the speed and manoeuvrability to evade a source of predation for which they have not evolved (Ford et al. 2001).

**Conclusion**

Characterising gene flow in natural and anthropogenically disturbed environments will become increasingly critical to conservation, especially for species like the southern scrub-robin for whom agriculture intersects a large part of their distribution. Here we have assessed dispersal through natural
and agricultural landscape types for the southern scrub-robin, a species facing challenges characteristic of many Australian species. We have demonstrated that landscape types that do not provide the necessary structural requirements impede gene flow and increase population genetic structure above and beyond distance alone. In the contemporary environment, the impact of some of these landscapes on dispersal may have been amplified by the presence of introduced predators such as the fox, against which ground-dwelling species such as the southern scrub-robin rely on vegetative cover for protection.

While the use of landscape genetics to understand the effect of habitat loss on population structure is widespread, very few studies have been completed on avian species to date (Haig et al. 2011). However where landscape genetic studies have been conducted, Australian birds in a variety of habitats demonstrate both strong preferences for dispersal habitat (e.g. Pavlacky et al. 2009) and reduced gene flow across habitat gaps (e.g. Amos et al. 2012) particularly in species of low mobility. These few studies demonstrate both the vulnerability of gene flow in Australian birds with low mobility to habitat loss, and highlight a knowledge gap that could prove critical in our ability to protect species from climate change. Dispersal attributes are central to a species ability to maintain gene flow and hence genetic diversity that enables adaptation, or effect range shifts in response to climate change. Landscape genetics studies of Australian avian (and undoubtedly other) species are needed urgently as the basis for judicious conservation plans.

Perhaps most urgently a better understanding of dispersal is required for arid avian species, such as the southern scrub-robin, for whom the effects of climate change may be particularly perilous. Preliminary studies in the northern hemisphere suggest that lowland desert-dwelling bird species may be at greater threat than montane species from contemporary climate change (Peterson et al. 2002, Peterson 2003). Furthermore, habitat quality and connectivity are already more likely to be diminished in lowland habitats, as extensive human disturbance is less prevalent in montane environments due to topographic restrictions (Hannah et al. 2002). If large reserves located on the fringe of productive agricultural land experience increasingly extreme climates, many arid species like the scrub-robin may find themselves forced to largely subsist within agricultural matrices containing only pockets of relictual habitat.
Understanding and improving the ability of the southern scrub-robin to disperse through and survive in such agricultural systems may well become the cornerstone of future conservation efforts for the species and many others like it. This study has identified which landscape types facilitate dispersal and can inform any future habitat restoration activities to improve gene flow (Chetkiewicz et al. 2006, Epps et al. 2007). Furthermore, our work can be used to help gauge novel conservation efforts such as the ability of native over introduced crops to enhance connectivity within the metapopulation (Collard and Fisher 2010).

If climate change does increase the reliance of some native species on agricultural regions, the time to act is now. More dispersal studies like this one are urgently needed for Australian bird species, and in particular arid species, as the basis for conservation planning and activities. Restoration activities require not only planning around the demography of the species concerned, but also land acquisition or landholder agreements for replanting or improving tracts of native vegetation. The growth and development of these ecosystems will require substantial time before they can fulfil their role as habitat and dispersal corridors for biodiversity into the future.

Acknowledgements

We acknowledge the assistance and support of Kathy Saint from the University of Adelaide and Alison Fitch from Flinders University. This project was funded by CSIRO (Climate Adaptation Flagship), Department of Environment and Natural Resources in South Australia (Wildlife Conservation Fund), Sir Mark Mitchell Research Foundation, Birds Australia (Stuart Leslie Bird Research Award) and Australian Geographic Society.
Chapter 6:

Home sweet home: habitat structure and invasive species drive patterns of local genetic diversity in the southern scrub-robin (Drymodes brunneopygia)

Jolene Scoble\textsuperscript{1,2}, J. Berton C. Harris\textsuperscript{3}, Peter Cale\textsuperscript{4}, Michael George Gardner\textsuperscript{1,5}, Anita K. Smyth\textsuperscript{6#} and Andrew John Lowe\textsuperscript{1,6,7*}

\textsuperscript{1} Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, North Terrace, Adelaide, SA 5005, Australia.

\textsuperscript{2} CSIRO, Climate Adaptation Flagship, GPO Box 1700, Canberra, ACT 2601, Australia.

\textsuperscript{3} Environment Institute, University of Adelaide, North Terrace, Adelaide, SA 5005, Australia.

\textsuperscript{4} Australian Landscape Trust, Calperum Station, PO Box 955, Renmark SA 5341

\textsuperscript{5} School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide 5001, Australia

\textsuperscript{6} CSIRO, PMB 2, Glen Osmond, SA 5064, Australia.

\textsuperscript{7} State Herbarium of South Australia, Science Resources Centre, Department of Environment and Natural Resources, Adelaide, SA 5005, Australia.

*Corresponding author: andrew.lowe@adelaide.edu.au

# Present address: Eco-informatics Facility, Terrestrial Ecosystem Research Network, University of Adelaide, North Terrace, SA 5005, Australia.

Running head: molecular implications of habitat quality for the southern scrub-robin

Article type: Empirical research
STATEMENT OF AUTHORSHIP

Home sweet home: habitat structure and invasive species are key aspects of habitat quality driving patterns of local genetic diversity in the southern scrub-robin (*Drymodes brunneopygia*)

This chapter has been prepared as a submission for publication.

**Jolene Scoble**
Sought and won funding, designed and executed field sampling, completed all laboratory work and data analysis, and prepared manuscript as principle author.

Signed:
Date: 27/01/2012

**J. Berton C. Harris**
Provided scripts for, and assistance with, data analysis and commented on manuscript.

Signed:
Date: 26/01/2012

**Peter Cale**
Assisted with design and execution of field sampling.

Signed:
Date: 21/01/2012

**Michael George Gardner**
Provided guidance on, and assisted with laboratory work and data analysis, and commented on manuscript.

Signed:
Date: 24/01/2012

**Anita Smyth**
Assisted with design and execution of field sampling, assisted with data analysis and commented on manuscript.

Signed:
Date: 19/01/2012
**Andrew John Lowe**
Assisted with design of field sampling, provided guidance on laboratory work and data analysis, and commented on manuscript.

Signed:
Date: 30/01/2012
Abstract

Characterising the drivers of population demography and spatial patterns of genetic diversity is an important foundation for developing conservation strategies. Given the current suite of novel, anthropogenic-forced threats to species persistence, understanding drivers of genetic diversity may be particularly important if we are to facilitate in situ adaptation to these threats. To date habitat loss has been the focus of conservation genetic studies, neglecting the role of habitat quality, which is frequently compromised by anthropogenic activities. We investigated genetic diversity and habitat quality using generalised linear models for the southern scrub-robin, a ground dwelling bird species endemic to the semi-arid mallee region of southern Australia. We report that a small subset of ecological variables measured, including reported abundance of invasive species (foxes and cats), amount of shrub and tree cover, number of weed species, and amount of leaf litter, were able to predict patterns of genetic diversity in four of the five metrics investigated. Diminished levels of genetic diversity were associated with high reported occurrences of foxes and cats by land managers, as well as surveyed weed infestations. The control of these invasive species should be a conservation priority for the southern scrub-robin. Our study also confirmed the fundamental requirement of a dense shrubby understorey for this species, suggesting that control of feral herbivores may also be of conservation benefit. Our results highlight the important role that habitat quality can play in determining genetic diversity, and the critical part that introduced species play in diminishing habitat quality.
**Introduction**

Genetic diversity is both a key measure of the impact of human activities on natural populations, and the raw material for species to adapt to future challenges (Lacy 1987, Riddle et al. 2008). Identifying and protecting environmental gradients that generate genetic diversity, and detecting the causes of declining genetic diversity have become major foci of conservation biology in the 21st century (Hendry et al. 2011, Lankau et al. 2011, Sgro et al. 2011). Anthropogenic habitat loss has been identified recurrently as a key determinant of heightened population structure and diminished genetic diversity. As a consequence, affected populations may have a compromised capacity to deal with novel environmental conditions and associated stress (Sgro et al. 2011). Habitat degradation, the process by which habitat quality is diminished over time, frequently occurs in concert with habitat loss (Mortelliti et al. 2010). Although we might expect changes in habitat quality to be stronger in fragmented systems where human activity is proximate and most prevalent, areas of intact vegetation may also suffer insidious, large scale loss of habitat quality when poorly managed (Hobbs et al. 2008).

While habitat quality is also recognised as a strong driver of individual fitness and population dynamics (Pulliam 2000), to date its effects have been largely overlooked in conservation action and research (Lindenmayer and Fischer 2007).

Habitat quality refers to the capacity of the environment to provide those conditions and resources that support individual persistence and reproduction (Hall et al. 1997). Heterogeneity in habitat quality thus induces strong selective pressure for discrimination among habitats of differing quality (Bowler and Benton 2005), and has the capacity to drive patterns of habitat occupancy (Mortelliti et al. 2010) and hence, genetic diversity. If poor habitat quality dissuades migrants from settling, microevolutionary processes such as gene flow that would otherwise maintain strong levels of genetic diversity and minimise inbreeding can be disrupted. Consequently, contemporary conservation planning requires an assessment of both natural and anthropogenic aspects of habitat quality in order to understand a species’ ability to respond *in situ* to novel environmental threats.
Contemporary habitat quality is often compromised by introduced species via direct competition and predation, as well as their effects on resource availability and structure. In the presence of invasive plant species, the abundance and diversity of native, resident plant species frequently decreases, altering plant community structure and decreasing the fitness and abundance of resident animal species (Vila et al. 2011). These changes are wrought as invasive plant species compete with resident species for access to, as well as changing the provision of a range of abiotic resources, including soil nutrients, light and moisture and temperature (Levine et al. 2003). For animal species, changes to habitat composition and structure will alter foraging opportunities, available microclimates, and the dynamics of competition and predation within the community (Levine et al. 2003, Pavey and Nano 2009, Litt and Steidl 2011). The movement and foraging activities of introduced herbivores can cause soil erosion, foul waterholes, support invasive predator populations, disperse weeds, and alter the extent, structure and composition of vegetation communities (Edwards et al. 2004). Introduced herbivores compete with native species for resources, and are frequently implicated in their decline (Edwards et al. 2004). Introduced predators often significantly add to predation pressure in the environment, because their prey has not had a sufficient time frame with which to develop specific predator defence mechanisms and avoidance strategies. Introduced predators may not only hunt adults, but substantially decrease reproductive success by targeting eggs and juveniles (Luck et al. 1999, Arthur et al. 2010).

Species with certain life-history attributes may be particularly susceptible to diminishing habitat quality. Ground dwelling species, which travel, forage and reproduce at the ground level may have a heightened vulnerability to changes in habitat quality, as such changes frequently occur first and most radically at ground level (Ford et al. 2001). Species with a reduced capacity for dispersal could also be at greater risk, as they may not be able to move away from areas of diminishing habitat quality, or have the capacity to locate areas of high habitat quality in the environment. The southern scrub-robin (Drymodes brunneopygia) is a ground dwelling, territorial avian species that is distributed throughout the semi-arid mallee region of southern Australia. We believe the southern scrub-robin is an ideal candidate to examine the effect of habitat quality on patterns of genetic diversity. Firstly, members of this species are only physically capable of short bursts of flight due to their short rounded wings, and
are well adapted to their ground dwelling habit as evidenced by their long tarsus and tail (Higgins and Peter 2002). Furthermore, while the scrub-robin is listed as of least concern (The Action Plan for Australian Birds 2000 (Garnett and Crowley 2000)) populations are disappearing from agricultural fragments and the species has a decreasing area of occupancy (Garnett and Crowley 2000, Cale and Mladovan 2007).

The primary aim of this study was to characterise both the amount and quality of habitat at the territorial scale relevant to southern scrub-robin fitness and survival that might explain variation in genetic diversity within the metapopulation. We hypothesise that increasing patch size, in particular that of essential habitat type (comprising a shrubby understorey) will increase genetic diversity. At sampling locations, we further hypothesise that vegetative cover, leaf litter and native plant biodiversity will also increase genetic diversity, while introduced predators and plant species will reduce genetic diversity.

**Materials and methods**

*Study species and system*

The southern scrub-robin is a medium-sized (21 – 42 g) ground dwelling bird species that has adopted a primarily sedentary lifestyle, maintaining a home territory for the purposes of foraging and reproduction (Higgins and Peter 2002). The scrub-robin’s life history is intimately dependent on the quality of ground habitat: it searches for food within the litter layer (invertebrates and seeds), nests on or close to the ground, and is heavily reliant on low shrubs for camouflage from mammalian and avian predators (Schodde 1981, Higgins and Peter 2002). The southern-scrub robin is known to avoid using, and nesting near, human made habitat edges, which may increase levels of predation (Luck et al. 1999), and it decreases in abundance where grazing has diminished vegetative ground cover (Cale and Mladovan 2007). We develop an ecological profile based upon empirical studies and expert opinion to characterise the necessary conditions and resources that individual southern scrub-robins require for survival and reproduction (Tables S6.1 and S6.2; supplementary information).
The southern scrub-robin is distributed throughout the semi-arid mallee region of southern Australia (Higgins and Peter 2002). The southerly regions of its distribution lie within areas comprised of fertile soils and climates most appropriate for agriculture, which has resulted in high levels of habitat loss and fragmentation. As a consequence there is often a mosaic of remnant habitat of varying size and geographical isolation in the southern regions of the scrub-robins distribution. In the northern areas of the southern scrub-robins’ distribution large regions of contiguous vegetation remain that are subject to commercial and/or feral grazing. Some former grazing properties have been purchased for conservation by government and non-for-profit organisations. Such is the case in Western and South Australia where our study regions are located.

**Sampling regions**

Between 11 and 22 (average 17) southern scrub-robins were sampled from locations in both agricultural mosaics and conservation parks at each of 17 locations during 2009 and 2010 (Figure 6.1). In Western Australia, five locations were sampled, four throughout the Wheatbelt region and one in the Shark Bay World Heritage Area. The Wheatbelt is a region of approximately 14 million hectares receiving between 280 and 600 mm of rainfall annually (Prober and Smith 2009). It was predominately cleared in the 1900s, of which 36% was cleared by 1920, and by 1984 clearing had peaked at 93% (Prober and Smith 2009). Shark Bay World Heritage Area covers some 2.2 million hectares, and was included on the World Heritage list in 1991 for its natural heritage values. In the east of the species’ range in South Australia, five populations were sampled within each of the Murray Mallee and Riverland Biosphere Reserve regions located in the Murray-Darling Rivers Basin, and two from the Flinders Ranges. The Murray Mallee comprises 1,836,000 hectares, of which 20% is currently remnant. Comparable with the clearing history of the Wheatbelt, around 31% of native vegetation was cleared in the Murray Mallee by 1930, with intensive clearing occurring until the 1980s (Willoughby 2006). The Riverland Biosphere Reserve lies directly north of the Murray Mallee region and is comprised of a suite of conservation properties that in the past were commercially grazed. The region is comprised of approximately 900,000 hectares, and is managed by both
Figure 6.1. Sampling locations of the southern scrub-robin across southern Australia (overview left pane). The central and right panes provide a detailed spatial representation of Western Australia and South Australian sample locations respectively. Areas cleared for human development, including agriculture are indicated by white shading, and areas maintaining native vegetation are shaded grey on each map. Dark grey indicates the presence of shrubby understorey, while light grey indicates the absence of a shrubby understorey. The wheatbelt region (receiving between 280 and 600mm of rainfall annually, in aqua) is outlined in Western Australia. In South Australia, the Flinders Ranges (orange) Murray-Darling Rivers Basin (red), Riverland Biosphere Reserve (green) and Murray Mallee (pink) are outlined.
government and non-for-profit agencies. The Flinders Ranges is the largest mountain range in South Australia. The area is 95,000 hectares in size and its highest point is 1,170m. Located in an area of otherwise low relief, the Flinders Ranges are proposed to have acted as a refugium, particularly for birds, during past climatically extreme periods (Byrne 2008a).

Sample and data collection

Individual birds were trapped using a 9 m long, 38 mm mesh size mist-net with the aid of a territorial vocalisations broadcast from a small speaker adjacent to the mist-net. A 28 gauge needle was used to draw a small amount (~5µl) of blood from each bird. Blood was captured using Whatman’s® FTA elute cards and stored at room temperature with silica. DNA extraction was carried out in accordance with the procedure specified by Whatman®. The DNA was stored at -20 ºC.

For each of the 17 sampling locations, three capture sites were randomly chosen at which to assess vegetation structure. The GPS coordinates marking the capture point of the southern scrub-robin/s at each site was used as the centre point for a 100 m point-intercept transect. Vegetation was classified into life-forms to emphasise function and structure as indicators of resources available to southern scrub-robins’ within the ecosystem rather than taxonomy. At each half metre interval, the presence of forbs (vegetation < 30 cm), shrubs (low-growing bushes > 30 cm, leaves present from ground level upward), and trees (plants > 30 cm, leaves not present at ground level) was recorded. Leaf litter was recorded at 10 metre intervals along the transect using a one metre-squared quadrat as an indicator of invertebrate (particularly ant) foraging opportunities. Leaf litter cover was measured and recorded in quartiles (1 = 0-24%, 2 = 25-49%, 3 = 50-74%, 4 =75-100%). Land managers at each location were asked to rate fox and cat sightings (defined as when searching for their presence as part of pest species management) as uncommon (rarely sighted, 0-1 individuals/hour, score = 1), moderate (often sighted, 2-3 individuals/hour, 2) or common (almost always sighted, >3 individuals/hour, 3). For South Australian locations, some additional information was collected. The capture point was also used as the centre of a 30 m x 30 m quadrat from which a vegetation species list was drawn up. This list was
comprised of both native and introduced plant species. We also sought to investigate the structure provided by spatially dominant species to scrub-robin habitat. The two dominant shrub species were identified (on the basis of occurrence), and where these species intercepted the half metre intervals on the point-interval transect their width and height were recorded.

Microsatellite genotyping and molecular data analysis

We genotyped individuals at 10 D. brunneopygia-specific microsatellite primers as outlined in Scoble et al. (2011), utilising the same polymerase chain reaction (PCR) mixture and conditions. Microsatellite alleles were scored using the program Genemapper® (version 3, Applied Biosystems) with manual checking. To calculate a genotyping error, we repeat-genotyped approximately 11% of samples for each marker, and calculated scoring errors per allele and per reaction for each locus and summarised across all loci (sensu Hoffman and Amos 2005).

Genotypes for each locus were subjected to population specific tests of linkage disequilibrium (Lewontin and Kojima 1960) and assessed for departures from Hardy-Weinberg equilibrium (Guo and Thompson 1992) due to heterozygote deficiency using ARLEQUIN 3.5.1.2 (Excoffier and Lischer 2010). The sequential Bonferroni procedure (Rice 1989) was applied to adjust significance levels (α = 0.05). MICRO-CHECKER was utilised to check for allele scoring errors due to stuttering and large allele drop out (Van Oosterhout et al. 2004).

Five different genetic indices were employed to understand the response of the southern scrub-robin to habitat quality: 1). We employed effective population size (Ne) to understand how reproductive success and population persistence respond to habitat quality. We calculated effective population size (Ne) using ONeSAMP (Tallmon et al. 2008), implemented via an online software interface (Koyuk et al. 2011). ONeSAMP infers effective population size from summary statistics calculated using microsatellite data within an approximate Bayesian framework. Onesamp creates 50, 000 simulated populations on the basis of user inputs, each of which has an effective size drawn from a uniform random number between the lower and upper Ne specified as priors by the user (Tallmon et al. 2008).
We specified a range for \( Ne \) of two to 200 for natural populations, and two to 100 for remnant populations under the assumption that remnant populations are smaller due to less available habitat and greater isolation. However preliminary testing revealed that the dataset was robust to changes in priors (up to a range of two to 1000). 2) **Genetic diversity** (measured as expected heterozygosity, \( He \)) describes the impact of effective population size on evenness of genetic variability. Observed (\( Ho \)) and expected (\( He \)) heterozygosity (Nei 1978) were calculated using ARLEQUIN (Excoffier and Lischer 2010). 3) The number of private alleles (\( PA \)) at a given sampling site provides an indication of its distinctiveness, and connectivity to other sampled locations (Kalinowski 2004). Number of **private alleles** (\( PA \)) were calculated using a rarefaction approach (Hurlbert 1971, Petit et al. 1998, Kalinowski 2004) in the program ADZE (Szpiech et al. 2008). The rarefaction method ensures the impact of unequal sample sizes on estimates is mediated by standardising all sample sizes so that each are equal to or less than the smallest sample size. 4) The **inbreeding coefficient**, \( F_{IS} \), measures departures from Hardy-Weinberg equilibrium within each population via the difference between observed and expected heterozygosity and provides a measure of population substructure (Wright 1951). \( F_{IS} \) (Wier and Cockerham 1984) was calculated using ARLEQUIN (Excoffier and Lischer 2010). 5) Lastly, population-specific \( F_{ST} \) was employed to evaluate population genetic structure relative to that of the sampled metapopulation (Foll and Gaggiotti 2006). Local \( F_{ST} \), a measure of allele frequencies for each site relative to that of global allelic patterns, was calculated using a hierarchical Bayesian approach implemented within the program GESTE (Foll and Gaggiotti 2006). The statistical significance of differences in genetic diversity (as measured by \( He \) and \( F_{IS} \)) between regions was calculated using FSTAT V2.9.3.2 (Goudet 1995).

**Ecological metric data preparation and analysis**

Patch size was derived using the National Vegetation Information System (NVIS) raster layer for extant vegetation (cell size 100 m x 100 m), provided by Australian Government Department of the Environment and Water Resources (DEWR 2006). Data for this raster later was compiled from a variety of state based sources, and was collected on ground between 1997 and 2004. All vegetation categories were reclassified into a single native vegetation class, and the raster layer converted to a
polygon shape file which allowed an area calculation for each polygon. Sampling location centroids were calculated as the mean of Universal Transverse Mercator (UTM) capture coordinates at each location. Each sampling location centroid was then used to identify the native vegetation patch in which that sample location was situated. Subsequently, the native vegetation class was subdivided into that with, and without a shrubby understorey in order to calculate the shrubby understorey patch size in which each sample location was situated.

The percentage of points at which each life form (forb, shrub and tree) was recorded during point-intersect transects was calculated for each sampling location. Leaf litter ordinal data was also averaged (median) across quadrats for each sampling location. For South Australian locations, dominant shrub species area was calculated as the average shrub volume \( \text{volume} = \pi r^2 h \) of the two most dominant shrub species per sample site within a given location. Native and introduced plant species were also averaged to give the respective number of species per sample site within a given location.

Assessing the relationships between ecological and genetic indices

Correlations among ecological predictor variables were assessed using Spearman’s rank correlation coefficient \( r_s \) for interval and ordinal variables in R v. 2.12.1 (R Development Core Team, 2005). Variables with a correlation above 0.65 were not used within the same model. The normality of predictor ecological variables was assessed via histograms and the Shapiro-Wilk normality test. Appropriate transformations (arcsine transformations for percentile data, and natural log transformations for all other data) were applied to data not normally distributed. The distribution of genetic response variables was also assessed using histograms of both the data itself and the residuals of the null model.

The relationship between ecological predictors and each genetic metric was assessed with Gaussian generalised linear models (GLMs) in R v. 2.12.1, utilising the MASS, lme4, Matrix, qpcR and boot packages (R Development Core Team, 2005). Information-theoretic model selection (Burnham and
Anderson 1998, 2001, 2002) was employed to assess models representing different competing hypotheses seeking to explain genetic diversity. Models were ordered according to their Akaike’s (1992) information criterion corrected for small sample size (AIC\(_c\)), and then ranked based upon their \(\Delta\text{AIC}_c\). We calculated model AIC\(_c\) weights (\(w_i\)) to assess the support for individual models. We choose to use AIC\(_c\) over dimension consistent criteria (e.g. BIC) because it is a more appropriate statistic for empirical biological data, particularly when sample size is small in relation to the number of estimated parameters (Burnham and Anderson 2002).

**Results**

**Evaluating loci**

Regenotyping of samples revealed scoring errors for loci DRYB15 (0.0167 per reaction, 0.0083 per allele), DRYB29 (0.0323 per reaction, 0.0161 per allele) and DRYB34 (0.0172 per reaction, 0.0086 per allele). Summarised across all loci, this equates to an error rate per reaction of 0.0071 and 0.0036 per allele. We found no evidence of scoring errors due to large allele drop-out or stuttering. Deviations from Hardy-Weinberg equilibrium at four loci (DRYB15, DRYB21, DRYB29, DRYB34) were evident at single sampling localities. Deviations from Hardy-Weinberg equilibrium (HWE) can be due to population level processes such as subpopulation structure (Wahlund effect), inbreeding, or due to the presences of null (non-amplified) alleles. The presence of null alleles is known to have a strong effect on genotype-based statistics such as \(F_{IS}\). Therefore as a secondary check of the loci’s deviating from HWE we calculated \(F_{IS}\) for each locus. We found that locus DRYB21 had an \(F_{IS}\) value of more than double that of any other locus. On the basis of these combined results, we eliminated locus DRYB21 from further analysis due to the probable presence of null alleles. All other loci were included in analyses. Linkage disequilibrium was detected for 5 locus pairs, comprising just 0.82% of total pairs assessed (36 locus comparisons for each of 17 populations). Because no one pair of loci was found to be in linkage disequilibrium (LD) in more than one sampling location, we attributed this result to population-specific genetic processes and no loci were excluded due to LD.
Patterns of genetic diversity

The number of alleles per locus ranged from four (DRYB46) to 17 (DRYB 33), with a mean of 10.11. All loci in all sampling locations were polymorphic. Levels of genetic diversity as estimated by $H_e$ showed little difference between states (average values; $H_e$: Western Australia 0.674, South Australia 0.680) (Table 6.2). The small difference in $H_e$ between states was not significant ($p = 0.727$). However Western Australia has an average value of $PA$ (0.18) almost three times that of South Australia (average: 0.06). Average $F_{IS}$ values indicate an excess of heterozygotes in Western Australia (-0.02), and on the contrary, a deficiency of heterozygotes in South Australia (0.08), which constituted a significant difference ($p = 0.006$).

Genetic diversity varied considerably within each state. In Western Australia, CG, the population with the smallest patch size had the lowest $H_e$ at 0.57 (Table 6.1). Dragon Rocks NR, the southern-most sampling location in Western Australia, had the highest $H_e$ (0.76). All Western Australian populations have a relatively high level of $PA$, except CG (0.08). Inbreeding levels (indicating population substructure) were generally low across the state; FP had the highest $F_{IS}$ value (-0.08). In South Australia those populations located in conservation parks north of the Murray River (Riverland Biosphere Reserve and Flinders Ranges) have on average lower levels of genetic diversity (average values for $H_e$ 0.67 and $PA$ 0.04) compared with those south of the river embedded in Murray Mallee agricultural matrix, including BR and YM (average values for $H_e$ 0.70, and $PA$ 0.09), although this trend was not significant ($p = 0.225$). This pattern was predominately driven by locations in the Flinders Ranges, AR and TG, which had the lowest levels of $H_e$ (0.60 and 0.61 respectively). Comparing only among agricultural Murray Mallee (average $He$ 0.70) with non-agricultural Riverland Biosphere Reserve (average $He$ 0.70) regions reveal very similar levels of genetic diversity that were not significant ($p = 0.836$). Billiatt CP South and North, southern-most in the Murray Mallee’s agricultural matrix, had the highest levels of $H_e$ (BS: 0.73, BN: 0.72). Two populations in the agricultural matrix had the highest values of $PA$, YM (0.12) and BS (0.15). However, the highest levels of population substructure were also found in the agricultural Murray Mallee (average $F_{IS}$: 0.10).
although there was no significant difference (p = 0.701) to inbreeding in the Riverland Biosphere Reserve (average $F_{IS}$: 0.06) and the Flinders Ranges (average $F_{IS}$: 0.08).

The highest $N_e$ values were also found in the southern, agriculturally dominated areas of both Western Australia and South Australia. In South Australia we found that the highest effective population sizes were within the Murray Mallee, at YM ($N_e = 30.10$, 95% CI = 23.30, 57.74) and BS ($N_e = 33.13$, 95% CI = 25.71, 58.36). The smallest $N_e$ value was also within the Murray Mallee, at BR ($N_e = 12.32$, 95% CI = 9.20, 20.67). In Western Australia, the most isolated sampling location, CG, had the highest effective population size ($N_e = 23.34$, 95% CI = 18.95, 37.25), followed by the northern-most location FP ($N_e = 19.17$, 95% CI = 15.40, 30.12).

**Ecological characteristics of sampling locations**

Most sampling locations in both South and Western Australia were found within a large area of contiguous native vegetation that forms the rangelands of central Australia (Table 6.2). In South Australia’s Murray Mallee, HB occupied the smallest patch of native vegetation (22728 ha), while BS and BN were both located in Billiatt Conservation Park, the largest remnant in the study, comprising 101,209 ha of native vegetation. In Western Australia, CG was located in the smallest remnant patch of native vegetation for the entire study (653 ha), while the sample site DR was found within a patch of some 33,295 ha. Shrubby vegetation patch size reflects a similar pattern to that of native vegetation patch size, with the smallest patches located in the agricultural matrices (CG: 653 ha, HB: 785 ha). However some sampling locations in contiguous vegetation were also found in small shrubby patches, such as DG (1445 ha).

Forb (South Australia: 9.87; Western Australia: 6.86) and tree (South Australia: 19.78; Western Australia: 2.32) cover were on average higher in South Australia, whilst shrub cover (South Australia: 34.98; Western Australia: 49.85) was higher in Western Australia (Table 6.2). Land managers rated both cat (South Australia: 1.25; Western Australia: 2.60) and fox (South Australia: 1.42; Western Australia: 1.80) sightings as occurring more frequently in Western Australia. In Western Australia,
Table 6.1 Measures of genetic diversity at 9 microsatellite loci in 12 South Australian (SA), and 5 Western Australian (WA) sampling locations. Each location is detailed with its name and abbreviation, region, number of birds sampled ($N$), effective population size ($Ne$), observed ($Ho$) and expected ($He$) heterozygosities, private alleles ($PA$), fixation index ($F_{IS}$) and population genetic structure ($F_{ST}$).

<table>
<thead>
<tr>
<th>State</th>
<th>Location</th>
<th>Abbreviation</th>
<th>Region</th>
<th>$N$</th>
<th>$Ne$</th>
<th>$Ho$</th>
<th>$He$</th>
<th>$PA$</th>
<th>$F_{IS}$</th>
<th>$F_{ST}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SA</td>
<td>Arkaroo Rock</td>
<td>AR</td>
<td>Flinders Ranges</td>
<td>17</td>
<td>19.01</td>
<td>0.50</td>
<td>0.60</td>
<td>0.08</td>
<td>0.16</td>
<td>0.22</td>
</tr>
<tr>
<td></td>
<td>Telowie Gorge</td>
<td>TG</td>
<td>Flinders Ranges</td>
<td>17</td>
<td>18.09</td>
<td>0.60</td>
<td>0.61</td>
<td>0.03</td>
<td>0.01</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td>Yookamurra Sanctuary</td>
<td>YM</td>
<td>Murray Mallee</td>
<td>18</td>
<td>30.10</td>
<td>0.62</td>
<td>0.69</td>
<td>0.12</td>
<td>0.09</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>Brookfield CP</td>
<td>BR</td>
<td>Murray Mallee</td>
<td>11</td>
<td>12.32</td>
<td>0.55</td>
<td>0.67</td>
<td>0.07</td>
<td>0.20</td>
<td>0.12</td>
</tr>
<tr>
<td></td>
<td>Henry's Block</td>
<td>HB</td>
<td>Murray Mallee</td>
<td>18</td>
<td>21.35</td>
<td>0.57</td>
<td>0.67</td>
<td>0.07</td>
<td>0.15</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>Froggy Dam</td>
<td>FD</td>
<td>Riverland Biosphere Reserve</td>
<td>17</td>
<td>21.27</td>
<td>0.66</td>
<td>0.70</td>
<td>0.02</td>
<td>0.06</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>Long Dam</td>
<td>LD</td>
<td>Riverland Biosphere Reserve</td>
<td>18</td>
<td>20.24</td>
<td>0.63</td>
<td>0.69</td>
<td>0.04</td>
<td>0.09</td>
<td>0.08</td>
</tr>
<tr>
<td></td>
<td>Taylorville Station</td>
<td>TS</td>
<td>Riverland Biosphere Reserve</td>
<td>16</td>
<td>18.67</td>
<td>0.63</td>
<td>0.71</td>
<td>0.07</td>
<td>0.11</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>Hideaway Block</td>
<td>HD</td>
<td>Riverland Biosphere Reserve</td>
<td>18</td>
<td>23.92</td>
<td>0.67</td>
<td>0.70</td>
<td>0.10</td>
<td>0.03</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>BilliattCP South</td>
<td>BS</td>
<td>Murray Mallee</td>
<td>22</td>
<td>33.13</td>
<td>0.66</td>
<td>0.73</td>
<td>0.15</td>
<td>0.09</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>BilliattCP North</td>
<td>BN</td>
<td>Murray Mallee</td>
<td>16</td>
<td>19.63</td>
<td>0.74</td>
<td>0.72</td>
<td>0.05</td>
<td>-0.03</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Dangalli CP</td>
<td>DG</td>
<td>Riverland Biosphere Reserve</td>
<td>19</td>
<td>22.69</td>
<td>0.69</td>
<td>0.67</td>
<td>0.01</td>
<td>-0.03</td>
<td>0.07</td>
</tr>
<tr>
<td>WA</td>
<td>Dragon Rocks NR</td>
<td>DR</td>
<td>Wheatbelt</td>
<td>16</td>
<td>15.38</td>
<td>0.73</td>
<td>0.76</td>
<td>0.23</td>
<td>0.01</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Charles Gardner NR</td>
<td>CG</td>
<td>Wheatbelt</td>
<td>16</td>
<td>23.34</td>
<td>0.57</td>
<td>0.57</td>
<td>0.08</td>
<td>0.01</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>Mt Gibson Sanctuary</td>
<td>MG</td>
<td>Wheatbelt</td>
<td>14</td>
<td>15.70</td>
<td>0.74</td>
<td>0.73</td>
<td>0.17</td>
<td>-0.03</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>Kalbarri NP</td>
<td>KB</td>
<td>Wheatbelt</td>
<td>14</td>
<td>14.16</td>
<td>0.69</td>
<td>0.67</td>
<td>0.17</td>
<td>-0.03</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>Francois Peron NP</td>
<td>FP</td>
<td>Shark Bay World Heritage Area</td>
<td>14</td>
<td>19.17</td>
<td>0.69</td>
<td>0.64</td>
<td>0.23</td>
<td>-0.08</td>
<td>0.14</td>
</tr>
</tbody>
</table>
Table 6.2 Ecological metrics calculated across all locations sampled for southern scrub-robins. Native vegetation and shrubby understorey patch sizes are calculated in hectares, forb, shrub and tree cover values are the percentage of sampled points where each were found, average leaf litter index is the average quartile value (1 = 0-24%, 2 = 25-49%, 3 = 50-74%, 4 = 75-100%) of 1m x 1m quadrat surveyed leaf litter, fox and cat sightings are land manager observances (1 = uncommon, 2 = moderately common, 3 = very common). An * indicates data were not normally distributed and was transformed appropriately prior to analysis.

<table>
<thead>
<tr>
<th>State</th>
<th>Location</th>
<th>Native vegetation patch size (hectares)*</th>
<th>Shrubbery understorey patch size (hectares)*</th>
<th>Forb cover (%)*</th>
<th>Shrub cover (%)</th>
<th>Tree cover (%)*</th>
<th>Average leaf litter index</th>
<th>Fox sightings*</th>
<th>Cat sightings*</th>
</tr>
</thead>
<tbody>
<tr>
<td>SA</td>
<td>Arkaroo Rock</td>
<td>624,324,715</td>
<td>1,549,247</td>
<td>5.31</td>
<td>39.97</td>
<td>34.16</td>
<td>3.00</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Froggy Dam</td>
<td>624,324,715</td>
<td>488,017</td>
<td>3.98</td>
<td>14.43</td>
<td>12.11</td>
<td>1.64</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Long Dam</td>
<td>624,324,715</td>
<td>488,017</td>
<td>8.79</td>
<td>30.85</td>
<td>25.54</td>
<td>2.18</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Taylorville Station</td>
<td>624,324,715</td>
<td>488,017</td>
<td>3.15</td>
<td>26.53</td>
<td>29.35</td>
<td>2.48</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Hideaway Block</td>
<td>624,324,715</td>
<td>488,017</td>
<td>13.60</td>
<td>41.13</td>
<td>41.63</td>
<td>2.58</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Telowie Gorge</td>
<td>624,324,715</td>
<td>113,410</td>
<td>20.73</td>
<td>51.41</td>
<td>13.60</td>
<td>2.81</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Yookamurra Sanctuary</td>
<td>624,324,715</td>
<td>21,802</td>
<td>29.02</td>
<td>27.03</td>
<td>9.78</td>
<td>1.85</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Brookfield CP</td>
<td>624,324,715</td>
<td>23,963</td>
<td>11.44</td>
<td>22.55</td>
<td>14.26</td>
<td>2.30</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Dangalli CP</td>
<td>624,324,715</td>
<td>1,445</td>
<td>12.94</td>
<td>42.45</td>
<td>10.12</td>
<td>2.03</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>BilliattCP South</td>
<td>101,209</td>
<td>96,720</td>
<td>1.66</td>
<td>49.59</td>
<td>12.60</td>
<td>2.55</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>BilliattCP North</td>
<td>101,209</td>
<td>96,720</td>
<td>6.14</td>
<td>49.75</td>
<td>13.10</td>
<td>2.45</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Henry's Block</td>
<td>22,728</td>
<td>785</td>
<td>1.66</td>
<td>24.05</td>
<td>21.06</td>
<td>2.18</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>WA</td>
<td>Mt Gibson Sanctuary</td>
<td>624,324,715</td>
<td>7,332,747</td>
<td>0.66</td>
<td>44.78</td>
<td>2.32</td>
<td>2.85</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Kalbarri NP</td>
<td>624,324,715</td>
<td>7,332,747</td>
<td>0.66</td>
<td>56.38</td>
<td>0.00</td>
<td>2.61</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Francois Peron NP</td>
<td>624,324,715</td>
<td>7,332,747</td>
<td>4.48</td>
<td>35.66</td>
<td>0.00</td>
<td>2.00</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Dragon Rocks NR</td>
<td>33,295</td>
<td>32,200</td>
<td>24.54</td>
<td>56.88</td>
<td>9.29</td>
<td>2.00</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Charles Gardner NR</td>
<td>653</td>
<td>653</td>
<td>3.98</td>
<td>55.56</td>
<td>0.00</td>
<td>2.33</td>
<td>2</td>
<td>3</td>
</tr>
</tbody>
</table>
vegetation cover was on average highest in the southern sampling locations DR and CG embedded in the agricultural area (forb: 14.26; shrub: 56.22; tree: 4.65) compared with northern locations (MG, KB and FP) on the fringe of the Wheatbelt (forb: 1.93; shrub: 45.61; tree: 0.77), while leaf litter was comparable across all Western Australia sites. Foxes and cats were observed more frequently in northern agricultural fringe locations (fox: 2; cat: 2.67) than DR and CG embedded in the Wheatbelt (fox: 1.5; cat: 2.5). Within South Australia, leaf litter and vegetation cover were comparable between the agricultural Murray Mallee region, and areas of contiguous vegetation in the Riverland Biosphere Reserve and Flinders Ranges, although tree cover was on average higher in non-agricultural areas (agricultural: 14.16; non-agricultural: 23.79). Foxes (agricultural: 1.6; non-agricultural: 1.3) were observed more frequently in the agricultural Murray Mallee when compared with non-agricultural areas, while cats were observed at consistently low rates across both regions (agricultural: 1.2; non-agricultural: 1.3). Dominant shrub species volume, average number of weeds and natives were all

Table 6.3 Ecological metrics measured only for southern scrub-robs sampled in South Australia. Dominant shrub species area measures the average shrub area of the two most dominant shrub species per sample site within a given location. Native and introduced plant species are the average number of respective species per sample site within a given location. An * indicates that data were not normally distributed and was transformed appropriately.

<table>
<thead>
<tr>
<th>Location</th>
<th>Dominant shrub species area (m$^2$)*</th>
<th>Introduced plant species (weeds)* (mean per site)</th>
<th>Native plant species (mean per site)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Telowie Gorge</td>
<td>7,397.18</td>
<td>3.67</td>
<td>18.00</td>
</tr>
<tr>
<td>Arkaroo Rock</td>
<td>6,415.87</td>
<td>3.00</td>
<td>23.67</td>
</tr>
<tr>
<td>Dangalli CP</td>
<td>4,762.45</td>
<td>0.33</td>
<td>30.00</td>
</tr>
<tr>
<td>Long Dam</td>
<td>1,882.09</td>
<td>2.33</td>
<td>29.67</td>
</tr>
<tr>
<td>Froggy Dam</td>
<td>1,731.21</td>
<td>0.67</td>
<td>30.00</td>
</tr>
<tr>
<td>BilliattCP South</td>
<td>1,509.24</td>
<td>0.00</td>
<td>16.33</td>
</tr>
<tr>
<td>Taylorville Station</td>
<td>1,417.53</td>
<td>1.33</td>
<td>24.67</td>
</tr>
<tr>
<td>Hideaway Block</td>
<td>668.66</td>
<td>0.00</td>
<td>19.67</td>
</tr>
<tr>
<td>Yookamurra Sanctuary</td>
<td>361.76</td>
<td>1.67</td>
<td>18.67</td>
</tr>
<tr>
<td>Henry's Block</td>
<td>158.57</td>
<td>0.00</td>
<td>14.00</td>
</tr>
<tr>
<td>Brookfield CP</td>
<td>153.43</td>
<td>2.33</td>
<td>16.67</td>
</tr>
<tr>
<td>BilliattCP North</td>
<td>152.81</td>
<td>0.00</td>
<td>16.33</td>
</tr>
</tbody>
</table>
Table 6.4 Models of ecological metrics weighted by their effect on effective population size \((N_e)\), expected \((H_e)\) heterozygosity, private alleles \((P_A)\), fixation index \((F_{IS})\) and population genetic structure \((F_{ST})\) for the southern scrub-robin in South Australia. Ecological metrics within each model indicate the direction of influence (+ or -) on genetic diversity. Statistics presented include number of parameters \((K)\), Akaike’s information criterion corrected \((AIC_c)\), \(AIC_c\) weights \((w_i)\), and the percentage deviance explained in the genetic metric by the model \((% \text{ deviance explained})\). Only models with a \(\Delta AIC_c \leq 4\) or \(\Delta AIC_c \geq \) of the null model (1) are displayed.

<table>
<thead>
<tr>
<th>Measure of genetic diversity</th>
<th>Ecological metric one</th>
<th>Ecological metric two</th>
<th>(K)</th>
<th>(\Delta AIC_c)</th>
<th>(w_i)</th>
<th>% deviance explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N_e \sim)</td>
<td>-Fox sightings</td>
<td>null</td>
<td>3</td>
<td>0.00</td>
<td>0.37</td>
<td>36.04</td>
</tr>
<tr>
<td></td>
<td>null</td>
<td></td>
<td>2</td>
<td>1.70</td>
<td>0.16</td>
<td>-</td>
</tr>
<tr>
<td>(H_e \sim)</td>
<td>-Fox sightings</td>
<td>-Weeds</td>
<td>3</td>
<td>0.00</td>
<td>0.24</td>
<td>46.22</td>
</tr>
<tr>
<td></td>
<td>-Weeds</td>
<td></td>
<td>3</td>
<td>0.11</td>
<td>0.23</td>
<td>45.71</td>
</tr>
<tr>
<td></td>
<td>-Cat sightings</td>
<td></td>
<td>3</td>
<td>1.56</td>
<td>0.11</td>
<td>38.74</td>
</tr>
<tr>
<td></td>
<td>-Leaf litter</td>
<td>-Weeds</td>
<td>4</td>
<td>1.90</td>
<td>0.09</td>
<td>57.47</td>
</tr>
<tr>
<td></td>
<td>-Shrub cover</td>
<td>-Weeds</td>
<td>4</td>
<td>3.27</td>
<td>0.05</td>
<td>52.32</td>
</tr>
<tr>
<td></td>
<td>null</td>
<td></td>
<td>2</td>
<td>3.78</td>
<td>0.03</td>
<td>-</td>
</tr>
<tr>
<td>(P_A \sim)</td>
<td>null</td>
<td></td>
<td>2</td>
<td>0.00</td>
<td>0.23</td>
<td>-</td>
</tr>
<tr>
<td>(F_{IS} \sim)</td>
<td>+ Leaf litter</td>
<td>-Shrub cover</td>
<td>4</td>
<td>0.00</td>
<td>0.65</td>
<td>69.52</td>
</tr>
<tr>
<td>(F_{ST} \sim)</td>
<td>+Leaf litter</td>
<td>+Weeds</td>
<td>4</td>
<td>0.00</td>
<td>0.29</td>
<td>70.93</td>
</tr>
<tr>
<td></td>
<td>+Weeds</td>
<td></td>
<td>3</td>
<td>0.15</td>
<td>0.27</td>
<td>56.39</td>
</tr>
<tr>
<td></td>
<td>+Fox sightings</td>
<td></td>
<td>3</td>
<td>1.59</td>
<td>0.13</td>
<td>50.85</td>
</tr>
<tr>
<td></td>
<td>+Tree cover</td>
<td>+Weeds</td>
<td>4</td>
<td>2.11</td>
<td>0.10</td>
<td>65.33</td>
</tr>
<tr>
<td></td>
<td>+Cat sightings</td>
<td></td>
<td>3</td>
<td>3.51</td>
<td>0.05</td>
<td>42.312</td>
</tr>
</tbody>
</table>
Figure 6.2 Relationship between effective population size ($N_e$) (A), expected heterozygosity ($H_e$) (B), fixation index ($F_{IS}$) (C) and population genetic structure ($F_{ST}$) (D) and the ecological variable which best explains each for the southern scrub-robin in South Australia.
Table 6.5. Top ecological models explaining patterns of effective population size (\(N_e\)), expected (\(H_e\)) heterozygosity, fixation index (\(F_{IS}\)) and population genetic structure (\(F_{ST}\)) for the southern scrub-robin in South Australia. As the top model for private alleles (\(P_A\)) is the null model (1), no model is displayed. Information presented includes each models ecological metric/s, together with their estimates and 95% confidence intervals (in brackets), intercept, and residual error.

<table>
<thead>
<tr>
<th>Measure of genetic diversity</th>
<th>Ecological metric one</th>
<th>Estimate (95% CI)</th>
<th>Ecological metric two</th>
<th>Estimate (95% CI)</th>
<th>Intercept</th>
<th>Residual error</th>
</tr>
</thead>
<tbody>
<tr>
<td>(N_e \sim)</td>
<td>Fox sightings</td>
<td>-8.06 (-12.66, -2.08)</td>
<td></td>
<td></td>
<td>23.90</td>
<td>4.57</td>
</tr>
<tr>
<td>(H_e \sim)</td>
<td>Fox sightings</td>
<td>-0.07 (-0.15, -0.03)</td>
<td></td>
<td></td>
<td>0.70</td>
<td>0.03</td>
</tr>
<tr>
<td>(F_{IS} \sim)</td>
<td>Shrub cover</td>
<td>-0.006 (-0.009, -0.003)</td>
<td>Leaf litter</td>
<td>0.15 (0.05, 0.22)</td>
<td>-0.04</td>
<td>0.04</td>
</tr>
<tr>
<td>(F_{ST} \sim)</td>
<td>Weeds</td>
<td>0.06 (0.01, 0.09)</td>
<td>Leaf litter</td>
<td>0.06 (-0.02, 0.11)</td>
<td>-0.08</td>
<td>0.03</td>
</tr>
</tbody>
</table>

higher in the non-agricultural areas (shrub area: 3467.86; weeds: 1.62; natives: 25.10) compared with the agricultural region (shrub area: 467.16; weeds: 0.80; natives: 16.40) (Table 6.3). We found no relationship between the number of weed species, and the number of native plant species present within a sampling location (\(y = 0.5221x + 20.806, R^2 = 0.0134\)).

Assessing competing models explaining genetic diversity

Initially we conducted GLM’s including data from all sampled locations in Western and South Australia. It appeared that state-based differences in habitat and genetic diversity were predominately driving results as opposed to overarching relationships, and further investigation of the data using scatter plots confirmed this. We therefore decided to proceed with data from South Australia alone in model analysis. As we only sampled five locations in Western Australia, it was not possible to complete a robust GLM analysis of this data separately.
In South Australia a small suite of ecological variables were consistently found in the best models for all genetic diversity metrics except $PA$, which did not have a relationship with any of the measured ecological metrics that improved upon the null model (Table 6.4). However, the directionality of the relationships these important ecological metrics had with individual measures of genetic diversity did not always conform to our hypotheses. Leaf litter was associated with increased $F_{IS}$ and $F_{ST}$, and decreased $He$ while shrub cover was associated with decreased $He$ and tree cover was found to increase levels of $F_{ST}$. However these effects all occurred within bivariate models and the relationships were not strong enough alone to substantiate a univariate model for any of the genetic diversity measures with a $\Delta AICc$ above four or as an improvement over the null model.

Fox sightings was the best model for both $Ne$ ($\beta = -8.06$, SE = 3.40, CI = -12.66, -2.08) and $He$ ($\beta = -0.07$, SE = 0.02, CI = -0.15, -0.03), wherein increasing fox abundance was associated with increasing levels of both metrics. Confidence intervals around each estimate did not cover zero (Table 6.5, Figure 6.2). A bivariate model including shrub cover (negative relationship) and leaf litter (positive relationship) was the top model explaining $F_{IS}$ (shrub cover: $\beta = -0.006$, SE = 0.001 (-0.009, -0.003); leaf litter: $\beta = 0.15$, SE = 0.04 (0.05, 0.22)), also with confidence intervals around each estimate that did not cover zero. The best model for $F_{ST}$ was also bivariate, weeds ($\beta = 0.06$, SE = 0.02, CI = 0.01, 0.09) and leaf litter ($\beta = 0.06$, SE = 0.03, CI = -0.02, 0.11) increased genetic structure. Confidence intervals for leaf litter that do cover zero within this model indicate that weeds were the most meaningful ecological metric. We investigated data from Western Australia to see if the trends demonstrated in top South Australian models were present, and found that only the relationship between $F_{IS}$ and shrub cover (adjusted $R^2 = 0.7219$, $F_{1,3} = 11.38$, $p = 0.04330$) held.

Discussion

The capacity of habitat to provide the resources and conditions necessary for the survival and reproduction of resident plants and animals, referred to as habitat quality, is a critical driver of population demography. Habitat quality is likely to influence dispersing individuals searching for a home site, shaping patterns of occupancy (Bowler and Benton 2005), and ultimately playing a crucial
role in the spatial configuration of genetic diversity within the metapopulation. Despite a surge of interest in the drivers of genetic diversity for conservation planning (Hendry et al. 2011, Lankau et al. 2011, Sgro et al. 2011), the role of habitat quality has received little attention in conservation literature (Lindenmayer and Fischer 2007).

We investigated habitat quality and patterns of genetic diversity across agricultural and conservation areas in Western Australia and South Australia for the southern scrub-robin, a ground-dwelling avian species distributed across southern Australia. An integrated approach investigating the effects of both within and between site habitat characteristics would have given a more complete overview of the drivers of genetic diversity. However here we build upon previously completed work on the relationship between genetic structure and between site habitat characteristics, at a broader scale (unpublished data, Chapter Five). Habitats occupied by southern scrub-robins in each state were found to be fundamentally different; Western Australian habitats were characterised by higher shrub cover and higher sightings of introduced predators, particularly cats, while in South Australia forb and tree coverage was comparably higher. Analysing only in South Australia with GLM, we found a subset of ecological variables including fox and cat sightings, shrub and tree cover, weed species, and leaf litter predicted patterns of genetic diversity in four of the five metrics of genetic diversity we investigated with varying degrees of confidence. None of the ecological metrics we measured was able to explain variation in PA. The number of private alleles indicates the distinctness of the sampling unit from others investigated. We generally reported low levels of PA in South Australia, suggesting that gene flow is substantial enough throughout the study area that distinctness among sample sites is equivocal. Low levels of PA are likely to have precluded any strong relationship with the ecological variables measured.

The role of introduced species
Anthropogenic activities frequently result in changes to native vegetation composition or biodiversity. This equates to a decrease in habitat quality for some species, and consequently may be associated with decreased levels of local genetic diversity (Scribner et al. 2001, Lin et al. 2008). Increasing numbers of weeds were associated with decreasing levels of both $He$ and increasing $F_{ST}$ for the southern scrub-robin. While weeds are often implicated in declining diversity of native plant species (Vila et al. 2011) we failed to find any relationship between the plant biodiversity and number of weed species. However this does result does not negate the possibility that in the presence of weeds, plant biodiversity at our study sites has decreased from historic levels. The presence of weeds is also known to alter foraging opportunities, and ecosystem process, such as nutrient cycling, hydrology or fire (Levine et al. 2003). Weeds are often less palatable to both herbivores and insects (DiTomaso 2000, Mitchell et al. 2006) and as a consequence their presence at study sites may have reduced fruits, seeds and insects available for consumption by southern scrub-robins.

Increased sighting frequency of both cats and foxes were predicted to be associated with comparatively lower levels of genetic diversity in the southern scrub-robin. Fox and cat predation have been identified as a key cause of decline in of many Australian animals including ground dwelling birds in southern Australia (Ford et al. 2001, Priddel et al. 2007). Furthermore, foxes have been identified as a specific threat to reproductive success in the southern scrub-robin, particularly near human-derived habitat edges (Luck et al. 1999). As predicted, we detected a negative correlation between fox and cat sightings and $He$. The presence of foxes and cats may reduce genetic diversity by decreasing population size and limiting successful immigration. Fox predation has been implicated in both these demographic trends for the quokka (Setonix brachyurus) at sites in Western Australia (Hayward et al. 2005). Fox and cat sightings also have a positive relationship with $F_{st}$, indicating that foxes and cats may indeed have an isolating effect on populations, decreasing immigration and hence increasing population structure in areas where they are prevalent. Increased fox sightings were also correlated with decreasing levels of $Ne$, suggesting that foxes may be implicated with decreasing local effective population size (Frankham 1995) by rendering it an unattractive site for migrants and/or predating southern scrub-robins. As $Ne$ is related to $He$ through the relationship $4N_e\mu = H_e/(1 - H_e)$
(Kimura and Ohta 1971), the potential of foxes to have an effect on both these metrics comes as no surprise.

Size, structure and biodiversity of habitats

While our hypotheses regarding the relationship between invasive species and metrics of genetic diversity were confirmed, for other aspects of habitat quality results were somewhat counterintuitive. Patch size, forb cover, dominant shrub species area, and number of native plant species all failed to explain the patterns of genetic diversity in any of the metrics we investigated. While forb cover may contribute to foraging opportunities, we did not discriminate between native and non-native species, and for this reason may have confounded the effect of weeds and native forb cover. In the absence of any relationship between native species based metrics and genetic diversity, our results tentatively suggest that habitat structure (irrespective of contributing species) is a better measure of habitat quality for the southern scrub-robin. Nonetheless, habitat composition is often an important aspect of habitat quality (Scribner et al. 2001, Lin et al. 2008), and warrants further investigation for this species. Lastly, neither measure of patch size had a relationship on genetic diversity, but perhaps this is most surprising for Ne. Effective population size, through its relationship with population size (Frankham 1995), is dependent on the carrying capacity of the environment and can be strongly related to habitat amount (e.g. Wang et al. 2011). We may have failed to capture the exact aspects of the environment which constitute appropriate habitat to the southern scrub-robin, or alternatively, other aspects of population demography may be at play, such as patch connectivity (Frankham 1995).

Tree cover did not increase genetic diversity as expected, but was correlated with increasing Fst, and hence decreasing habitat quality. Trees play an important role in southern scrub-robin habitat; they provide a high point for territorial vocalisations and observations (Higgins and Peter 2002), a refuge from ground-dwelling predators such as the fox, and by increasing the structural complexity of the habitat, they may increase invertebrate biomass available for foraging (Andersen 1983, Dangerfield et al. 2003). However large trees, especially eucalypts, compete with understory plants and hence decrease shrub cover, an essential component of southern scrub-robin habitat. Increasing tree cover
beyond a certain threshold may reduce habitat quality for southern scrub-robin. Results from this study confirm a negative relationship between tree and shrub cover in southern scrub-robin habitat.

Increasing levels of leaf litter were also associated with increasing $F_{st}$, in addition to increasing levels of $F_{IS}$. Leaf litter is an important foraging substrate for many ground dwelling birds. However, high levels of leaf litter may be indicative of increased tree cover, and hence decreased habitat quality for the southern scrub-robin. Alternatively, some or all of the ant fauna that comprise a large part of the diet of the southern scrub-robin may not rely on leaf litter as part of their habitat or may only use litter produced by specific tree species. Hence leaf litter may not be the most appropriate way to measure foraging opportunities for this species. Leaf litter sampling may fail to detect many species of Australian ants (Oliver and Beattie 1996). The foraging ecology of the southern scrub-robin and its relationship to habitat quality requires further study.

We report conflicting results for shrub cover, an ecological metric we considered to be a fundamental aspect of habitat quality for this species. Shrub cover had a negative effect on $H_e$, within a bivariate model with weeds. Further investigation of this relationship demonstrated the confidence intervals of the estimate for this model cover zero, indicating that the directionality of the relationship with $H_e$ is equivocal. Conversely, we see the strongest relationship of the study between $F_{IS}$ and shrub cover, in the negative direction hypothesised. In both South Australia and Western Australia, as shrub cover increases, levels of population substructure converge on zero confirming the fundamental nature of understorey structure for this ground dwelling species. Shubby understorey provides protection from climatic extremes, foraging opportunities, and protection from predators, and is known to be a critical aspect of habitat quality for many species of ground-dwelling birds (Sieving et al. 1996, Reid et al. 2004, Castellon and Sieving 2006, Tomasevic and Estades 2008, Pavlacky et al. 2009, Manhaes and Dias 2011).
Conclusion

Understanding the drivers of genetic diversity is a fundamental basis for contemporary conservation planning, as by building and protecting genetic diversity, we provide species with the best chance of successfully responding in situ to novel environmental challenges. Our study indicates that habitat quality, particularly those aspects affected by invasive species, is an important driver of local patterns of genetic diversity for the southern scrub robin. Both weed infestations and fox and cat sightings were correlated with decreasing genetic diversity and their improved control could increase habitat quality for the southern scrub-robin and likely other native species in eastern South Australia. Furthermore, we confirmed the central nature of a shrubby understorey to habitat quality for this species, the condition and amount of which may be improved with the removal of feral herbivores such as goats, which are prevalent in many areas of eastern South Australia. While we did not investigate the contribution of feral herbivores to habitat quality within this study, their detrimental effects on native vegetation are well documented (Edwards et al. 2004). Improving habitat quality for species like the southern scrub-robin is a cost-effective way to strengthen metapopulations and the microevolutionary processes that sustain them. While ongoing protection of biodiversity through land acquisition for conservation should remain a priority; its effectiveness in that role can be drastically compromised by invasive species and other drivers of diminished habitat quality. Understanding the nature of, and seeking to improve habitat quality for native species is an important partner to successful conservation.

Acknowledgements

We acknowledge the assistance and support of Kathy Saint from the University of Adelaide and Alison Fitch from Flinders University. This project was funded by CSIRO (Climate Adaptation Flagship), Department of Environment and Natural Resources in South Australia (Wildlife Conservation Fund), Sir Mark Mitchell Research Foundation, Birds Australia (Stuart Leslie Bird Research Award) and Australian Geographic Society.
Supplementary section

Table S6.1. Ecological site variables, their influence on predation risk, food availability and other factors, and hypothesised relationship with genetic indices for the southern scrub-robin (*Drymodes brunneopygia*) in Western and South Australia. Genetic indices include effective population size (*Ne*), expected (*He*) heterozygosity, private alleles (*PA*), fixation index (*F*<sub>IS</sub>) and population genetic structure (*F*<sub>ST</sub>).

<table>
<thead>
<tr>
<th>Habitat metric</th>
<th>Predation risk</th>
<th>Food availability</th>
<th>Other factors</th>
<th>Hypothesised relationship with <em>He</em> and <em>Ne</em></th>
<th>Hypothesised relationship with <em>PA</em>, <em>F</em>&lt;sub&gt;ST&lt;/sub&gt; and <em>F</em>&lt;sub&gt;IS&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native vegetation patch size</td>
<td>Visual and structural protection and decreasing edge:area with increasing size</td>
<td>Increased potential foraging opportunities with increasing size</td>
<td>None</td>
<td>+ve</td>
<td>+ve</td>
</tr>
<tr>
<td>Shrubby understorey vegetation patch size</td>
<td>Highest level of visual and structural protection</td>
<td>Habitat heterogeneity and comparatively high moisture levels facilitate excellent foraging opportunities</td>
<td>Positive relationship with effective population size; increased chance of finding a mate and reproducing</td>
<td>+ve</td>
<td>+ve</td>
</tr>
<tr>
<td>Forb cover</td>
<td>None</td>
<td>Increasing forb biomass increases fruit and seed availability, and increases the abundance of invertebrates.</td>
<td>None</td>
<td>+ve</td>
<td>+ve</td>
</tr>
<tr>
<td>Shrub cover</td>
<td>Visual and structural protection provided by the fundamental aspect of habitat</td>
<td>Increasing shrub biomass improves fruit and seed availability, and increases the abundance of invertebrates directly and via leaf litter</td>
<td>Increasing shrub cover may signal better habitat quality and result in increased reproductive opportunities and success</td>
<td>+ve</td>
<td>+ve</td>
</tr>
<tr>
<td>Tree cover</td>
<td>Ability to take shelter in tree branches to avoid foxes</td>
<td>Increasing tree biomass improves the abundance of invertebrates directly and via leaf litter</td>
<td>Provide perches for territorial singing/observations. Competes with shrubby understorey to decrease amount of shrub habitat.</td>
<td>+ve</td>
<td>-ve</td>
</tr>
<tr>
<td>Leaf litter cover</td>
<td>Camouflage for snakes</td>
<td>Foraging substrate for invertebrates which are southern scrub-robin’s primary food source</td>
<td>None</td>
<td>+ve</td>
<td>+ve</td>
</tr>
<tr>
<td>Fox density</td>
<td>Ground predator</td>
<td>None</td>
<td>None</td>
<td>-ve</td>
<td>-ve</td>
</tr>
<tr>
<td>Cat density</td>
<td>Able to predate on ground and in trees</td>
<td>None</td>
<td>None</td>
<td>-ve</td>
<td>-ve</td>
</tr>
</tbody>
</table>
Table S6.2 Ecological site variables, their influence on predation risk, food availability and other factors, and hypothesised relationship with genetic indices for the southern scrub-robin (*Drymodes brunneopygia*) in South Australia only. Genetic indices include effective population size (*Ne*), expected (*He*) heterozygosity, private alleles (*PA*), fixation index (*F_{IS}*), and population genetic structure (*F_{ST}*).

<table>
<thead>
<tr>
<th>Habitat metric</th>
<th>Predation risk</th>
<th>Food availability</th>
<th>Other factors</th>
<th>Hypothesised relationship with <em>He</em> and <em>Ne</em></th>
<th>Hypothesised relationship with <em>PA</em>, <em>F_{ST}</em> and <em>F_{ST}</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant shrub species area</td>
<td>Primary contributor of visual and structural protection</td>
<td>Primary contributor to fruit and seed availability, important contributor toward invertebrate biomass</td>
<td>Increasing area of dominant shrub type may signal better habitat quality and result in increased reproductive opportunities and success</td>
<td>+ve</td>
<td>+ve</td>
</tr>
<tr>
<td>Number weed species</td>
<td>Indicator of habitat disturbance, and poor habitat management</td>
<td>Potential to compete with native food sources</td>
<td>None</td>
<td>-ve</td>
<td>-ve</td>
</tr>
<tr>
<td>Number native species</td>
<td>Indicator of habitat health and sound management</td>
<td>Facilitates diverse diet directly through fruits and seeds, and indirectly through invertebrate diversity</td>
<td>None</td>
<td>+ve</td>
<td>+ve</td>
</tr>
</tbody>
</table>
Table S6.3 Spearman’s rank correlation for ecological metrics calculated across South Australian locations sampled for southern scrub-robins (*Drymodes brunneopygia*). Underlined values indicate those that exceed the cut-off value of 0.65. Ecological metrics with a correlation ≥ 0.65 were not placed in a model together for GLM analysis.

<table>
<thead>
<tr>
<th></th>
<th>Native vegetation patch size</th>
<th>Shrubby understory patch size</th>
<th>Forb cover</th>
<th>Shrub cover</th>
<th>Tree cover</th>
<th>Dominant shrub species area</th>
<th>Average leaf litter index</th>
<th>Introduced plant species</th>
<th>Native plant species</th>
<th>Fox sightings</th>
<th>Cat sightings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Native vegetation patch size</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrubby understory patch size</td>
<td>0.46</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forb cover</td>
<td>0.60</td>
<td>-0.09</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrub cover</td>
<td>-0.18</td>
<td>0.01</td>
<td>0.28</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tree cover</td>
<td>0.11</td>
<td>0.59</td>
<td>-0.19</td>
<td>-0.06</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dominant shrub species area</td>
<td>0.48</td>
<td>0.44</td>
<td>0.13</td>
<td>0.31</td>
<td>0.04</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average leaf litter index</td>
<td>-0.02</td>
<td>0.47</td>
<td>-0.04</td>
<td>0.55</td>
<td>0.64</td>
<td>0.26</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Introduced plant species</td>
<td>0.68</td>
<td>0.35</td>
<td>0.40</td>
<td>-0.08</td>
<td>0.12</td>
<td>0.53</td>
<td>0.19</td>
<td>*</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Native plant species</td>
<td>0.76</td>
<td>0.47</td>
<td>0.20</td>
<td>-0.21</td>
<td>-0.02</td>
<td>0.58</td>
<td>-0.30</td>
<td>0.31</td>
<td>*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fox sightings</td>
<td>-0.03</td>
<td>-0.14</td>
<td>0.00</td>
<td>-0.17</td>
<td>0.29</td>
<td>0.02</td>
<td>0.34</td>
<td>0.48</td>
<td>-0.41</td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>Cat sightings</td>
<td>-0.29</td>
<td>0.06</td>
<td>-0.40</td>
<td>-0.17</td>
<td>0.40</td>
<td>0.11</td>
<td>0.27</td>
<td>0.08</td>
<td>-0.22</td>
<td>0.54</td>
<td>*</td>
</tr>
</tbody>
</table>
Chapter 7:

Mapping the future: understanding how the environment shapes the distribution and genetic diversity of the southern scrub-robin (*Drymodes brunneopygia*)

Jolene Scoble¹,², Peter Cale³, Simon Ferrier⁴, Michael George Gardner¹,⁶, Bert Harris⁵, Thomas Harwood⁴, Andrew John Lowe¹,⁷,⁸, Anita Smyth⁷ and Kristen Williams⁴*

¹ Australian Centre for Evolutionary Biology and Biodiversity, University of Adelaide, North Terrace, Adelaide, SA 5005, Australia.
² CSIRO, Climate Adaptation Flagship, GPO Box 1700, Canberra, ACT 2601, Australia.
³ Australian Landscape Trust, Calperum Station, PO Box 955, Renmark SA 5341
⁴ CSIRO Ecosystem Sciences, GPO Box 1700, Canberra, ACT 2601, Australia
⁵ Environment Institute, University of Adelaide, North Terrace, Adelaide, SA 5005, Australia.
⁶ School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide 5001, Australia
⁷ Eco-informatics Facility, Terrestrial Ecosystem Research Network, University of Adelaide, North Terrace, SA 5005, Australia.
⁸ State Herbarium of South Australia, Science Resources Centre, Department of Environment and Natural Resources, Adelaide, SA 5005, Australia.

*Corresponding author: kristen.williams@csiro.au

Running head: molecular and demographic implications of climate change for the southern scrub-robin

Article type: Empirical research
STATEMENT OF AUTHORSHIP

Mapping the future: understanding how the environment shapes the distribution and genetic diversity of the southern scrub-robin (*Drymodes brunneopygia*)
This chapter has been prepared as a submission for publication.

**Jolene Scoble**
Sought and won funding, designed and executed field sampling, completed all laboratory work and data analysis, and prepared manuscript as principle author.

Signed:
Date: 27/01/2012

**Peter Cale**
Assisted with design and execution of field sampling.

Signed:
Date: 21/01/2012

**Simon Ferrier**
Provided guidance on, and assistance with data analysis.

Signed:
Date: 30/01/2012

**Michael George Gardner**
Provided guidance on, and assistance with laboratory work and data analysis, and commented on manuscript.

Signed:
Date: 24/01/2012

**J. Berton C. Harris**
Provided assistance with data analysis and commented on manuscript.

Signed:
Date: 26/01/2012
Thomas Harwood
Performed GDM under climate change analysis based on JS GDM models. Helped to write and produce figures for manuscript. Provided 0.01° climate change surfaces.

Signed: 
Date: 24/01/2012

Anita Smyth
Provided guidance on conceptual approach, assisted with design and execution of field sampling, and commented on manuscript.

Signed: 
Date: 19/01/2012

Andrew John Lowe
Assisted with design of field sampling, provided guidance on laboratory work and data analysis, and commented on manuscript

Signed: 
Date: 30/01/2012

Kristen Williams
Generated spatial environment data, provided guidance on and assistance with data analysis, and helped write manuscript.

Signed: 
Date: 22/01/2012
Abstract

It is not possible to protect all species from ubiquitous, human-wrought changes to the environment. How then is it feasible to protect such species from extinction? From this challenge springs one of the most important conservation questions of our time: how and where should we seek to facilitate in situ adaptation to changing environmental conditions? Climate change is one key threat to species persistence, and facilitating adaptation to climate change can enhance species conservation. In order to facilitate adaptation it is necessary to understand the role of environmental variables and spatial patterns of genetic diversity. We investigate the role that substrate, climate and habitat resources play in shaping both occupancy patterns, and spatial patterns of genetic diversity in the southern scrub-robin (Drymodes brunneopygia).

The southern scrub-robin is a ground dwelling, territorial avian species that is distributed across semi-arid southern Australia. Distributional modelling suggests that spatial patterns of occupancy have a strong relationship to the environmental variables (particularly water availability and habitat resources) investigated and that climate change may result in an increase in the area of suitable habitat for the southern scrub-robin over the coming century. As a species of limited mobility however, the southern scrub-robin is unlikely to benefit widely from largely distant and inaccessible additions of suitable habitat. Rather, we suggest that facilitating in situ resilience and adaptation to changing conditions are important management options for the conservation of this species. Using Generalised Dissimilarity Modelling (GDM) to simultaneously consider the effects of distance and the environment, we identify substrate and temperature conditions among the most important environmental variables associated with spatial patterns of genetic diversity. To prioritise regions for additional conservation actions, we consider predicted genetic uniqueness, land use, climate suitability and the amount of pressure existing genetic-climate relationships are expected to experience. On the basis of these considerations, we suggest that central and south Western Australia, and south east and west South Australia should benefit most from enhanced conservation initiatives, as these regions are best placed to maintain a large effective population size and serve as centres of adaptation in the future.
Introduction

The natural world has undergone substantial modifications wrought by an ever-expanding and consumptive human population. Unfortunately, returning ecosystems to a real or imagined state that existed prior to modern human disturbance is, in most cases, an unrealistic goal (Thomas 2011). Likewise, it is impossible to protect species from all the current and future changes that human society will undoubtedly visit upon them, particularly anthropogenic climate change (Alkemade et al. 2009). While limiting our intrusion into the natural world where possible is unquestionably an important part of contemporary conservation, in many instances, species must adapt to environmental changes, or perish (Hoffmann and Sgrò 2011). From this challenge, springs one of the most important conservation questions of our time: how and where should we seek to facilitate *in situ* adaptation to changing environmental conditions?

Climate change represents a key threat to species persistence, where survival can be facilitated by adaptation to novel conditions. While climate change is hardly a new phenomenon, anthropogenic-driven climate change is occurring at a rate unprecedented in recent history (Burrows et al. 2011), and its impact will occur in ecosystems already suffering fragmentation and other perturbations associated with human activities (Mackey et al. 2008). There is now substantive evidence that anthropogenic climate change is responsible for shifting the climatic envelope of species around the world. For example, shifts in species climatic envelopes range shifts have been overwhelmingly observed in the direction expected due to climate change and species-specific physiological limits (Root et al. 2003, Tingleya et al. 2009, Chen et al. 2011). In response, conservation strategies that consider the impacts of climate change have largely focussed on the role that protected areas can play in supporting species during range shifts (Mawdsley 2011). However, it is likely that not all species will be able to track their climatic envelope (Parmesan 2006). During periods of extreme climatic aridity in Australia throughout the Pleistocene, many species, particularly those of low mobility, did not contract to major refugia. Phylogeographic studies instead indicate that such species frequently persisted in multiple, localised refugia throughout their range (Byrne 2008a). Localised persistence may have been facilitated by the availability of adequate habitat for viable populations, by phenotypic plasticity
and/or adaptation via genetic drift to changing conditions (Byrne 2008a). In the contemporary context, species may struggle to track their climatic envelope for a range of reasons. These includes the expected rapidity of climate change, inherent lack of mobility, a matrix hostile to dispersal due to land cover type or biotic interactions, and lack of habitat in climatically suitable areas. Facilitating adaptation to climate change clearly has an important role to play in conservation planning for the coming century (Prober et al. 2012).

Evolutionary potential has typically been incorporated into conservation planning by identifying and protecting areas of high phylogenetic diversification (Faith 1992). Regions where high concentrations of diverse phylogenetic lineages are located, as identified by long phylogenetic branch lengths, are often prioritised for conservation (e.g. Isaac et al. 2007). Phylogenetic diversity in this context is assumed to be an appropriate surrogate for past diversification of traits and hence, also future adaptive potential (e.g. Forest et al. 2007). Alternatively, the environmental gradients responsible for generating ongoing diversification within a taxonomic group may represent an appropriate conservation surrogate if evolutionary processes are sufficiently understood (e.g. Rouget et al. 2006). While characterising and protecting species level phylogenetic diversity has its own inherent conservation value, management strategies for facilitating adaptation to current and future climates need to also consider intraspecific genetic diversity. Intraspecific genetic diversity, which is frequently the result of recent microevolutionary processes, is expected to be a strong indication of current and future evolutionary potential (Thomassen et al. 2010, Thomassen et al. 2011).

The availability of environmental data, generated via ground truth, aerial and satellite remote-sensing, and climate monitoring in a high resolution spatial format, enables the identification of environmental gradients that drive species distributions and intraspecific adaption via spatially heterogeneous, divergent selection (Smith et al. 2008, Pease et al. 2009, Thomassen et al. 2010, Smith et al. 2011, Thomassen et al. 2011). Here we make use of such data sets, seeking to understand the relationship that the southern scrub-robin (*Drymodes brunneopygia*), a ground dwelling Australo-Papuan robin (Passeriformes: Petroicidae), has with the environment for a conservation planning purpose. Initially, we develop an ecological profile of the southern scrub-robin based upon empirical studies and expert
opinion, to guide decision making in the modelling process (Figure 7.1) (Austin 2002). We hypothesise that soil characteristics, precipitation, evaporation, temperature, wind, cloudiness, radiation and land use regulate resources available to the southern scrub-robin and hence will drive habitat boundaries and patterns of genetic diversity (Table 7.1). We examine these relationships under current climate conditions and subsequently under four future climate change scenarios to identify potential changes to the southern scrub-robins’ habitat envelope and regions that may facilitate adaptation to climate change.

Materials and methods

Study species and sampling regions

The southern scrub-robin is a medium-sized (21 – 42 g) ground dwelling bird species distributed throughout the semi-arid mallee shrubland region of southern Australia (Higgins and Peter 2002). While described as an omnivore, the majority of its diet consists of ants and other invertebrates (Higgins and Peter 2002). Southern scrub-robins are primarily sedentary and maintain a home territory in which they forage and reproduce (Higgins and Peter 2002). The scrub-robin’s life history intimately depends on the health of ground habitat; it searches for food within the litter layer (invertebrates and seeds), nests on or close to the ground, and relies on low shrubs for camouflage from mammalian and avian predators (Schodde 1981, Higgins and Peter 2002). The southern-scrub robin is known to avoid using, and nesting near, anthropogenic habitat edges, which may increase levels of predation (Luck et al. 1999). Additionally, the species decreases in abundance where grazing has diminished vegetative ground cover (Cale and Mladovan 2007).

Between 11 and 22 (average 17) southern scrub-robins were sampled from each of 17 locations across the species’ range during 2009 and 2010 (Figure 7.2). In Western Australia, five locations were sampled throughout the Wheatbelt region (Francois Peron National Park is situated north of the Wheatbelt in the Shark Bay World Heritage Area). The sampling locations (listed from south to north; abbreviations shown in Figure 7.2) are Dragon Rocks Nature Reserve (DR), Charles Gardner Nature
Reserve (CG), Mt Gibson Sanctuary (MG), Kalbarri National Park (KB) and Francois Peron National Park (FP). Clearing in the Wheatbelt peaked at 93% in the 1980’s (Prober and Smith 2009). In the east of the species’ range in South Australia, five populations were sampled within each of the Murray Mallee and Riverland Biosphere Reserve regions located in the Murray-Darling Rivers Basin, and two from the Flinders Ranges. In the Murray Mallee these locations are Billiatt Conservation Park north (BN) and south (BS), Brookfield Conservation Park (BR), Yookamurra Sanctuary (YM) and Henry’s block (HB). Yookamurra Sanctuary and Brookfield Conservation Park are ostensibly outside the Murray Mallee, however they occur in a similar agricultural setting and within the mallee vegetation community. The Murray Mallee comprises 1,836,000 hectares, of which 20% is extant native vegetation. In the Riverland Biosphere Reserve sample sites included Dangalli Conservation Park (DG), Froggy Dam (FD) and Long Dam (LD) within Gluepot Reserve (Birds Australia), and Hideaway block (HD) and Taylorville Station (TS) (Australian Landscape Trust).

![Figure 7.1 Flow diagram of resources and conditions that drive demography in the southern scrub-robin.](image)

Figure 7.1 Flow diagram of resources and conditions that drive demography in the southern scrub-robin. Thickness of arrows indicates strength of relationship. Hypotheses that underpin the relationships described by the flow chart (identified by abbreviations in arrow boxes) are detailed in Table 7.1.
Table 7.1 Ecological hypotheses outlining the resources and conditions that drive demography in the southern scrub-robin (linked with Figure 7.1)

<table>
<thead>
<tr>
<th>Relevant flow diagram arrow (Figure S7.1)</th>
<th>Ecological hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>P.1 AW.1 AW.2 AW.3 V.1 V.2 I.1</td>
<td><em>Precipitation</em> determines the recruitment, biomass and survivorship of vegetation in the semi-arid mallee region of southern Australia (Noble and Bradstock 1989). Vegetation provides foraging substrate, nesting materials and sites, protection from predators and extreme weather conditions (Higgins and Peter 2002). Insect (primary food source) diversity and abundance is positively correlated with rainfall itself, and indirectly with vegetation diversity in arid Australia (Andersen 1983, Dangerfield et al. 2003).</td>
</tr>
<tr>
<td>S.1 S.2 N.1 N.2 AW.1 AW.2 AW.3 V.1 V.2 I.1</td>
<td><em>Soil and landform</em> characteristics dictate the <em>plant available soil-water holding capacity</em> and <em>nutrient resources</em> that regulate recruitment, biomass and survivorship of vegetation in the semi-arid mallee region of southern Australia (Noble and Bradstock 1989).</td>
</tr>
<tr>
<td>T.1 T.2 AW.1 AW.2 AW.3 H.1 H.2 H.3 V.1 V.2 I.1</td>
<td><em>Temperature</em> is likely to impose restrictions on distribution directly via thermal tolerance, and also indirectly via its influence on insect activity and vegetation patterns (Higgins and Peter 2002), supplying important food resources.</td>
</tr>
<tr>
<td>E.1 E.2 C.1 C.2 C3 R.1 R.2 R.3 AW.1 AW.2 AW.3 H.1 H.2 H.3 AR.1 V.1 V.2 I.1</td>
<td><em>Solar radiation</em> and <em>cloudiness</em> also influence ambient temperature conditions, <em>evaporative</em> demand and water balance, and so indirectly influences recruitment, biomass and survivorship of vegetation in the semi-arid mallee region of southern Australia (Specht and Jones 1971, Specht 1981).</td>
</tr>
<tr>
<td>V.1 V.2 I.1</td>
<td><em>Vegetation productivity</em> (<em>growth indices</em>) determines structural habitat characteristics, as well as food availability through seasonal supply of fruits and seeds, as well as indirectly affecting insect diversity and abundance, which are important free water sources for survival as well as energy. Human <em>land use</em> patterns limit or remove vegetation providing habitat, resulting in individual displacement or local population extinction (Higgins and Peter 2002).</td>
</tr>
</tbody>
</table>
Figure 7.2 Sampling locations of the southern scrub-robin across southern Australia (overview left pane). The central and right panes provide a detailed spatial representation of Western Australia and South Australian sample locations respectively. Areas cleared for human development, including agriculture are indicated by white shading, and areas maintaining native vegetation are shaded grey on each map. The wheatbelt region (receiving between 280 and 600mm of rainfall annually, in aqua) is outlined in Western Australia. In South Australia, the Flinders Ranges (orange) Murray-Darling Rivers Basin (red), Riverland Biosphere Reserve (green) and Murray Mallee (pink) are outlined.
The Riverland Biosphere Reserve lies directly north of the Murray Mallee region and comprises a suite of conservation properties that in the past were commercially grazed. In the Flinders Ranges we sampled at Arkaroo Rock (AR) in the north and Telowie Gorge (TG) in the south. The Flinders Ranges is the largest mountain range in South Australia. The area is 95,000 hectares in size and its highest point is 1,170m. Located in an area of otherwise low relief, the Flinders Ranges are proposed to have acted as a refugium, particularly for birds, during past climatically extreme periods (Byrne 2008a).

Sample collection and microsatellite genotyping

Individual birds were trapped using a 9 m long, 38 mm mesh size mist-net with the aid of territorial vocalisations broadcast from a small speaker adjacent to the mist-net. A 28 gauge needle was used to draw a small amount (~5µl) of blood from each bird. Blood was captured using Whatman’s® FTA elute cards and stored at room temperature with silica. DNA extraction was carried out in accordance with the procedure specified by Whatman®. The DNA was stored at -20 ºC.

We genotyped individuals at 10 D. brunneopygia-specific microsatellite primers as previously outlined by Scoble et al. (2011), utilising the same polymerase chain reaction (PCR) mixture and conditions. Microsatellite alleles were scored using the program Genemapper® (version 3, Applied Biosystems) with manual checking. To calculate a genotyping error, we repeat-genotyped approximately 11% of samples for each marker, and calculated scoring errors per allele and per reaction for each locus and summarised across all loci (sensu Hoffman and Amos 2005).

Genotypes for each locus were subjected to population specific tests of linkage disequilibrium (Lewontin and Kojima 1960) and assessed for departures from Hardy-Weinberg equilibrium (Guo and Thompson 1992) due to heterozygote deficiency using ARLEQUIN 3.5.1.2 (Excoffier and Lischer 2010). MICRO-CHECKER was utilised to check for allele scoring errors due to stuttering and large allele drop out (Van Oosterhout et al. 2004).
Environmental data

We used 0.01 grid resolution GIS layers of substrate (soil, lithology, and landform) and climatic environmental variables derived for use as predictor variables in biological models (Williams 2010a, b). The substrate layers were derived from a number of sources. Soil attribute layers are an interpretation of soil properties based upon the Atlas of Australian Soils (McKenzie and Hook 1992, McKenzie et al. 2000, Western and McKenzie 2004), and describe soil depth, percent clay content, nutrient availability, plant-available soil water holding capacity and hydraulic conductivity. An inherent rock fertility attribute was interpreted from the 1:1 million surface Geology of Australia (De Vries 2009 (pers. comm.), Raymond 2009). Geophysical data (magnetics and gravity) was sourced from Geoscience Australia (Petkovic and Milligan 2002, Bacchin et al. 2008). A weathering intensity index, also sourced from Geoscience Australia, is modelled from airborne gamma-ray spectrometry and relief (Wilford 2011). Terrain variables were derived from the 9 second Digital Elevation Model (DEM, version 3) (Hutchinson et al. 2008) and describe slope, elevation roughness, topographic wetness, and valley bottom and ridge top flatness and erosional surfaces (Wilson and Gallant 2000, Gallant and Dowling 2003).

Climate grids representing the current climate (based upon a 30-year historical record, mean-centred on 1990) were derived using a 0.01º grid of elevation derived from the national 9-second Digital Elevation Model (DEM, version 3) (Hutchinson et al. 2008) and the climate surfaces available with ANUCLIM (version 6) (Hutchinson and Xu 2000, Society 2011). The two future climate change scenarios based on IPCC AR4 emission trajectories (high impact; A1FI emissions scenario, high climate sensitivity, medium impact; A1B emissions scenario, medium climate sensitivity) (Nakicenovic et al. 2000) at two future time points (2030 and 2070) based on the CSIRO mk 3.5 global circulation model (Gordon et al. 2010), were downloaded as 0.25º climate grids from the CSIRO OzCLim website (www.csiro.au/ozclim) (Ricketts and Page 2007) and downscaled to 0.01º resolution using ANUCLIM (version 6) (Hutchinson and Xu 2000, Society 2011). Monthly climatic layers were summarised into a few statistics describing the mean and extremes of the annual variation for evaporation, precipitation, rainfall-modified solar radiation and temperature, rainfall seasonality
indices and derivatives of a simple tipping-bucket water balance model as described in Williams et al. (2010a, b) (supplementary section).

MaxEnt species distribution modelling

We used the maximum entropy method MaxEnt (Phillips et al. 2006) to model the current and future (under both climate change scenarios described above) geographic distributions of the southern scrub-robin. We chose MaxEnt as it has been shown to consistently outperform alternative species distribution modelling applications across a range of modelling scenarios when used with presence-only data (Elith et al. 2006). MaxEnt is a general purpose machine-learning method that relates environmental variables, to presence-only species occurrence data to predict or infer a distribution (Phillips et al. 2006). MaxEnt estimates the target distribution of a given species by finding the probability distribution of maximum entropy, subject to constraints derived from the relationship between occurrence and environmental data (Phillips et al. 2006). By using regularization parameters, MaxEnt is able to balance fit and model complexity to avoid overfitting models (Phillips et al. 2006, Elith et al. 2011).

Presence only, geo-referenced southern scrub-robin distribution data were obtained from the Atlas of Australian Birds database (Birds Australia 2011). This long-term national database collates records of avian observations from both a range of institutions and individuals across Australia, and offers a comprehensive set of occurrence records. We used 2919 geo-referenced locations based on observations between 1998 and 2010. Location points were vetted in v9.3.1 of the Atlas against the global land cover map, GlobCover 2009 v2.3 (ESA 2010) according to scrub-robin habitat requirements outlined in our ecological profile for the species (supplementary section). Distribution points that were located in water bodies (marine and freshwater), urban and cropping areas, and from outside their known distributional range (Higgins and Peter 2002) were removed from the dataset, leaving 1536 locations ostensibly within extant native vegetation.
The southern scrub-robin’s ecological profile was additionally used as the basis for choosing a subset of environmental variables to use in a model. A modest, biologically-appropriate candidate set of environmental variables is needed to prevent under- or over-fitting the model, which may result in spurious distribution predictions (Austin 2002, Austin 2007). We selected substrate variables that described soil nutrient availability, landform, plant-available soil water holding capacity and land use (GlobCover) (supplementary section). Climatic variables characterised precipitation, solar radiation, temperature, evaporation and vegetation growth indices (supplementary section).

We created and employed a mask derived from the Interim Biogeographic Regionalisation of Australia (IBRA, version 6.1, DEWHA 2004), in which our distributional data occurred, to serve as the larger region from which 10,000 background sample points were drawn. This background was a fair compromise between areas that were ecologically appropriate for the species (Higgins and Peter 2002), but did not too narrowly restrict the modelling extent (Elith et al. 2011). Additionally, because MaxEnt randomly samples cells, and not all grid cells in geographic format are of equal size in the unprojected Geocentric Datum of Australia 1994 (GDA94), we created and used a bias grid to inform MaxEnt of cell size variation (Elith et al. 2011). We left all other parameters as defaults in our model run, aside from 25% of samples as a random test percentage, and the use of linear/quadratic/product features to represent curvilinear transformations of the environmental variables. We chose not to use complex feature types because initial testing indicated this resulted in over-fitting, as assessed by the smoothness of response curves that depict how each environmental variable affects the MaxEnt prediction in the presence of other variables. Additionally, after our first model run we subsequently removed variables that showed only a weak relationship with the response variable, using a threshold of 0.1 test gain in a jacknife test of variable importance, and reran the model. We also ran MaxEnt using the maximised training sensitivity plus specificity threshold (Liu et al. 2005), the output of which was used to help interpret genetic-environment analyses.

To assess the goodness-of-fit of our best model, we calculated the area under the curve (AUC) of the receiver operating characteristic (ROC) curve. The contribution of individual environmental predictors was assessed via jacknife tests of variable importance. We constrained the model study area for the
purposes of background sampling to the Interim Biogeographic Regions for Australia in which our sampling locations were found, however we allowed MaxEnt to predict distributions to a wider region across southern and central Australia so as not to constrain predictions too narrowly. Maps of habitat suitability were produced in ArcGIS v9.3.1, using five evenly distributed colour classes, on the basis of logistic outputs generated by MaxEnt. Classes are referred to as very low suitability (grey; 0-0.2), low suitability (yellow; 0.2-0.4), average suitability (light orange; 0.4-0.6), high suitability (dark orange; 0.6-0.8), and very high suitability (red; 0.8-1).

**Generalised dissimilarity modelling**

We used generalised dissimilarity modelling (GDM; Ferrier 2002, Ferrier et al. 2007) to predict spatial patterns of genetic turnover in the southern scrub-robin across the landscape based upon current and future environmental gradients. GDM is statistical technique that predicts spatial patterns of biotic dissimilarity or turnover based upon both geographic distance and environmental gradients. An extension of matrix regression, GDM was designed to specifically accommodate non-linearity commonly encountered in biological relationships through the use of I-spline basis functions (Ferrier et al. 2007, Manion 2009). Firstly, GDM uses maximum likelihood estimation to relate biological dissimilarity (in our case the response variable is genetic dissimilarity) among pairs of sample sites to environmental predictors and geographic distance. This process produces a set of parameterized, nonlinear regression functions, of which only significant contributors to spatial patterns of biotic dissimilarity are retained as environmental predictors in the final model. Secondly, the predicted compositional dissimilarities are used as a basis for clustering grid cells into discrete classes using an unsupervised numerical classification (Ferrier et al. 2007). Areas of similar colour are predicted to be compositionally similar (Belbin et al. 1983). Such classes derived using biological data represent a form of constrained environmental classification and can be employed in conservation assessment and planning.

For the 10 *D. brunneopygia*-specific microsatellite primers, we calculated Nei’s D genetic distance (Nei 1972, 1978) as implemented in GenAlex 6 (Peakall and Smouse 2006) as a measure of genetic
dissimilarity for all pairs of sampling locations *sensu* Thomassen et. al. (2010). Each scrub-robin capture point within a sample location was used to sample the environmental layers (~1 km grids). This approach enables natural variation in the resource relationship with local habitat to be included and modelled.

We modelled current spatial patterns of genetic turnover separately for three regions; in the west of the species distribution (Western Australia wheatbelt; “WEST”), in the east (Flinders ranges, Riverland Biosphere and Murray Mallee all located in South Australia; “EAST”), and for these regions combined (“ALL”). We constrained the model study area to the Interim Biogeographic Regions for Australia (described above) in which our sampling locations were found. We used an expanded selection of environmental predictors with three *I*-splines (0th, 50th, and 100th percentiles) and tested for over-fitting by evaluating variable importance as the partial contribution to the percentage deviance explained, estimated from the change in deviance upon removal of that variable from the model. Different thresholds accommodated the different sample sizes and their predicted turnover (EAST=0.06, WEST=0.1, ALL=0.1). Successive variables were removed and the model refitted until the minimum criterion for change in deviance was met. The resulting models were used to project genetic turnover for the two future climate change scenarios. Model extrapolation was managed by post-hoc setting the maximum and minimum values of the *I*-splines to the data range encompassing current and future scenarios.

Maps of GDM results were depicted using 100 classes for the ALL and WEST regions, while for the EAST region model we specified 300 classes. Original GDM maps were cropped in ArcGIS v9.3.1 using a native vegetation map derived from the National Vegetation Information System (NVIS v3.1) raster layer for extant vegetation (cell size 100 m x 100 m), provided by the Australian Government Department of the Environment and Water Resources (DEWR 2006). The GDM map was subsequently clipped using the current predicted distribution of the southern scrub-robin produced in MaxEnt using the maximised training sensitivity plus specificity threshold to distinguish the likely presence of suitable habitat.
In order to assess the potential effects of a changing climate on the genetics of the southern scrub-robin, we used the GDM model output to calculate the dissimilarity between the present environmental conditions at each point, and the future environmental conditions at the same point. Whilst the interpretation of the purely spatial model is that of a straightforward expected dissimilarity, other considerations must be taken into account when applying the model over time. Critically, the temporal lag between when environmental change occurs and when its impact on spatial patterns of genetic diversity is observable (Lowe et al. 2004) may result in the realised dissimilarity due to environmental effects falling behind the expected dissimilarity. However there may be other effects outside the scope of the GDM model (such as fluctuating metapopulation size) which may increase genetic dissimilarity above that predicted. The results are therefore best viewed as potential genetic dissimilarity. Analyses were only conducted for the EAST and WEST regions separately using the locally derived GDM models, and show the potential genetic dissimilarity of each cell with its future self. In a treatment similar to that applied to the current spatial patterns of genetic turnover, GDM maps were cropped in ArcGIS v9.3.1 using native vegetation maps derived from NVIS (DEWR 2006), and subsequently the scrub-robin distribution predicted under the corresponding climate scenario and time point produced in MaxEnt.

**Results**

*Evaluating loci*

Repeated genotyping of samples revealed scoring errors for loci DRYB15 (0.0167 per reaction, 0.0083 per allele), DRYB29 (0.0323 per reaction, 0.0161 per allele) and DRYB34 (0.0172 per reaction, 0.0086 per allele). Summarised across all loci, this equates to an error rate per reaction of 0.0071 and 0.0036 per allele. We found no evidence of scoring errors due to large allele drop-out or stuttering. Deviations from Hardy-Weinberg equilibrium at four loci (DRYB15, DRYB21, DRYB29, DRYB34) were evident at single sampling localities. Deviations from Hardy-Weinberg equilibrium (HWE) can be due to population level processes such as subpopulation structure (Wahlund effect), inbreeding, or due to the presences of null (non-amplified) alleles. The presence of null alleles is known to have a
strong effect on genotype-based statistics such as $F_{IS}$. Therefore as a secondary check of the loci’s deviation from HWE we calculated $F_{IS}$ for each locus. DRYB21 had an $F_{IS}$ value of more than double that of any other locus. On the basis of these combined results, we eliminated locus DRYB21 from further analysis due to the likely presence of null alleles. All other loci were included in subsequent analyses. Linkage disequilibrium (LD) was detected for five locus pairs, comprising just 0.82% of total pairs assessed (36 locus comparisons for each of 17 populations). Because no one pair of loci was found to be in linkage disequilibrium in more than one sampling location, we attributed this result to population-specific genetic processes and no loci were excluded due to LD.

Genetic distance

Genetic distance between sampled locations ranged from almost zero (BS:BS 0.066) to very high values (highest TG:SB 0.709) (Table 7.2). On average, genetic distance was highest between regions (mean: 0.376; st. dev.: 0.121) when compared to distances within South Australia (mean: 0.211; st. dev.: 0.101) and Western Australia (mean: 0.303; st. dev.: 0.103) alone.

Relationship between distribution and environment

Both the AUC of the ROC curve ($AUC_{test}=0.920$) and the predicted current distribution for the southern scrub-robin (Figure 7.2) indicate the MaxEnt model fit the data well. The predicted current distribution is an excellent fit for occurrence record data, with only small predictions of low habitat suitability in south-western Victoria and eastern New South Wales, which are beyond its currently known distribution (Figure 7.3). The total test gain for the final model was 1.5307. The most important predictor category was water availability, for which individual variable contributions (jacknife test gain) summed to 2.123 (Table 7.3). Substrate variables contributed the least to the modelled distribution (jacknife test gain: 0.166).

The current distribution model predicts that the Wheatbelt region is dominated by patchy areas of low and average habitat suitability (Figure 7.3). Conversely, in the eastern extent of the modelled
### Table 7.2 Pairwise Nei’s D genetic distance estimates for 12 South Australian, and 5 Western Australian sampling locations

|       | AR   | TG   | YM   | BR   | HB   | FD   | LD   | TS   | HD   | BS   | BN   | DG   |       | DR   | CG   | MG   | KB   | SB   |
|-------|------|------|------|------|------|------|------|------|------|------|------|------|-------|------|------|------|------|------|------|
| AR    | -    | 0.449| -    |      |      |      |      |      |      |      |      |      |       |      |      |      |      |      |      |
| TG    |      | 0.349| 0.150| -    |      |      |      |      |      |      |      |      |       |      |      |      |      |      |      |
| YM    |      | 0.441| 0.350| 0.267| -    |      |      |      |      |      |      |      |       |      |      |      |      |      |      |
| BR    |      |      | 0.361| 0.140| 0.179| 0.191| -    |      |      |      |      |      |       |      |      |      |      |      |      |
| HB    |      |      |      | 0.300| 0.283| 0.269| 0.187| 0.149| -    |      |      |      |       |      |      |      |      |      |      |
| FD    |      |      |      |      | 0.422| 0.413| 0.283| 0.163| 0.147| -    |      |      |       |      |      |      |      |      |      |
| LD    |      |      |      |      |      | 0.287| 0.325| 0.141| 0.295| 0.209| 0.160| 0.192| -    |      |      |      |      |      |      |
| TS    |      |      |      |      |      |      | 0.308| 0.225| 0.125| 0.192| 0.122| 0.110| 0.117| -    |      |      |      |      |      |      |
| HD    |      |      |      |      |      |      |      | 0.392| 0.227| 0.116| 0.221| 0.085| 0.125| 0.145| 0.082| -    |      |      |      |      |
| BS    |      |      |      |      |      |      |      |      | 0.369| 0.288| 0.155| 0.213| 0.067| 0.130| 0.143| 0.155| 0.142| 0.066| -    |
| BN    |      |      |      |      |      |      |      |      |      | 0.319| 0.313| 0.224| 0.239| 0.083| 0.133| 0.163| 0.173| 0.117| 0.108| 0.080| -    |
| DG    |      |      |      |      |      |      |      |      |      |      | 0.421| 0.488| 0.263| 0.380| 0.270| 0.269| 0.193| 0.305| 0.276| 0.192| 0.190| 0.307| -    |
| DR    |      |      |      |      |      |      |      |      |      |      |      | 0.386| 0.549| 0.513| 0.508| 0.457| 0.375| 0.514| 0.449| 0.407| 0.385| 0.580| 0.331| -    |
| CG    |      |      |      |      |      |      |      |      |      |      |      |      | 0.403| 0.537| 0.293| 0.354| 0.234| 0.291| 0.199| 0.294| 0.315| 0.238| 0.144| 0.251| 0.116| 0.378| -    |
| MG    |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.640| 0.440| 0.327| 0.483| 0.386| 0.332| 0.221| 0.360| 0.295| 0.271| 0.226| 0.321| 0.243| 0.413| 0.260| -    |
| KB    |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0.410| 0.709| 0.476| 0.579| 0.446| 0.453| 0.428| 0.477| 0.514| 0.466| 0.310| 0.375| 0.242| 0.497| 0.226| 0.323| -    |
Table 7.3 Environmental predictors that met statistical and threshold criteria utilised in MaxEnt and/or GDM, with a description and units detailed for each. The relative contribution of each environmental predictor is provided for the MaxEnt distribution (jacknife of test gain) and GDM regions EAST, WEST and the regions combined (ALL) (contribution to explaining genetic dissimilarity, bound between 0 and 1).

<table>
<thead>
<tr>
<th>Predictor category</th>
<th>Predictor</th>
<th>Description</th>
<th>MaxEnt Distribution</th>
<th>WEST</th>
<th>EAST</th>
<th>ALL</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance</td>
<td>GEOGRAPHIC DISTANCE</td>
<td>Euclidean distance between sampling locations (km)</td>
<td>n/a</td>
<td>0.132</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Substrate</td>
<td>BNDENSITY</td>
<td>Solum average bulk density (Mg/m$^3$)</td>
<td>-</td>
<td>-</td>
<td>0.109</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>CALCRETE</td>
<td>Calcrete in or below soil profile (presence)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.066</td>
</tr>
<tr>
<td></td>
<td>COARSE</td>
<td>Soils dominated by coarse fragments including ironstone (class)</td>
<td>-</td>
<td>0.066</td>
<td>-</td>
<td>0.037</td>
</tr>
<tr>
<td></td>
<td>FERT</td>
<td>Inherent rock fertility (Rating)</td>
<td>0.166</td>
<td>-</td>
<td>0.012</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>MAGNETICS</td>
<td>Magnetic anomalies (nanoTesla, nT)</td>
<td>-</td>
<td>-</td>
<td>0.073</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>SOLDEPTH</td>
<td>Solum depth (surface and subsoil layers) (M)</td>
<td>-</td>
<td>0.134</td>
<td>0.224</td>
<td>0.046</td>
</tr>
<tr>
<td></td>
<td>SLOPE</td>
<td>Terrain slope (%)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.083</td>
</tr>
<tr>
<td></td>
<td>VALLEYBOTTOM</td>
<td>Proportion Valley bottoms (%)</td>
<td>-</td>
<td>-</td>
<td>0.053</td>
<td>0.025</td>
</tr>
</tbody>
</table>

| Substrate variable contribution | 0.166 | 0.200 | 0.362 | 0.366 |

Water availability

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Description</th>
<th>MaxEnt</th>
<th>WEST</th>
<th>EAST</th>
<th>ALL</th>
</tr>
</thead>
<tbody>
<tr>
<td>ADEFI</td>
<td>Minimum month precipitation deficit (mm)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ADEFX</td>
<td>Maximum month precipitation deficit (mm)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ARID_MAX</td>
<td>Maximum month aridity index (Dimensionless)</td>
<td>0.588</td>
<td>0.063</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EVAPM</td>
<td>Mean annual evaporation (mm)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.115</td>
</tr>
<tr>
<td>EVAPX</td>
<td>Maximum month evaporation (mm)</td>
<td>-</td>
<td>-</td>
<td>0.059</td>
<td>-</td>
</tr>
<tr>
<td>RAINI</td>
<td>Precipitation of the driest month (mm)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>RAINM</td>
<td>Mean annual rainfall (mm)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>variable</td>
<td>description</td>
<td>unit(s)</td>
<td>Water availability contribution</td>
<td>Temperature</td>
<td>Exposure</td>
</tr>
<tr>
<td>----------------</td>
<td>------------------------------------------------------------------</td>
<td>---------</td>
<td>---------------------------------</td>
<td>-------------</td>
<td>----------</td>
</tr>
<tr>
<td>RAINX</td>
<td>Precipitation of the wettest month (mm)</td>
<td>-</td>
<td>2.123</td>
<td>0.743</td>
<td>0.906</td>
</tr>
<tr>
<td>SRAIN1MP</td>
<td>Solstice rainfall seasonality ratio (Dimensionless)</td>
<td>-</td>
<td>0.079</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WDEF_MAX</td>
<td>Maximum month soil water deficit (mm)</td>
<td></td>
<td>0.212</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WDEF_MEAN</td>
<td>Mean annual soil water deficit (mm)</td>
<td></td>
<td>0.082</td>
<td></td>
<td></td>
</tr>
<tr>
<td>WDEF_MIN</td>
<td>Minimum month soil water deficit (mm)</td>
<td></td>
<td>0.049</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Water availability contribution</td>
<td></td>
<td></td>
<td>0.059</td>
<td>0.176</td>
<td>0.047</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td>0.415</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MAXTX</td>
<td>Maximum temperature hottest month (°C)</td>
<td></td>
<td>0.455</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MINTI</td>
<td>Minimum temperature coldest month (°C)</td>
<td></td>
<td>0.205</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TRNGA</td>
<td>Annual diurnal temperature range (°C)</td>
<td></td>
<td>0.176</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TRNGX</td>
<td>Maximum month diurnal temperature range (°C)</td>
<td></td>
<td>0.110</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature contribution</td>
<td></td>
<td></td>
<td>0.197</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exposure</td>
<td></td>
<td></td>
<td>1.161</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RADNI</td>
<td>Minimum month rainfall-modified solar radiation (MJ/m²/day)</td>
<td></td>
<td>0.603</td>
<td></td>
<td></td>
</tr>
<tr>
<td>RADNX</td>
<td>Maximum month rainfall-modified solar radiation (MJ/m²/day)</td>
<td></td>
<td>0.303</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exposure contribution</td>
<td></td>
<td></td>
<td>0.047</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat resources</td>
<td></td>
<td></td>
<td>0.023</td>
<td></td>
<td></td>
</tr>
<tr>
<td>MEGAGI</td>
<td>Growth index C3 macrotherm plants (index)</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MESOGI</td>
<td>Growth index C3 mesotherm plants (index)</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>GlobCover</td>
<td>Contemporary land use (categorical)</td>
<td>0.824</td>
<td>n/a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat resources contribution</td>
<td></td>
<td></td>
<td>0.023</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL number of variables in the model</td>
<td></td>
<td></td>
<td>11</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 7.3 Occurrence data and Maxent model results for predicted current environmental conditions and future climate change scenarios. The first row depicts occurrence data for the southern scrub-robin from the Birds Australia Atlas of Australian Birds database (Birds Australia 2011) and the predicted current distribution. Distributions under moderate (A1B) and high (A1FI) emissions scenarios are depicted for 2030 (second row) and 2070 (third row). Predicted distributions are logistic outputs and indicate occurrence probability in five evenly distributed classes from very low (grey, 0-0.2) through yellow, light orange, dark orange to very high (red, 0.8-1.0).

distribution, habitat predictions are dominated by average to high suitability, and exhibit a more clumped spatial pattern. Across the modelled area, very low (4,987,153 km²) and low (127,659 km²) habitat suitability dominate, and there are decreasing areas of habitat suitability for average (73,952 km²), high (27,972 km²) and very high (109 km²) classes. Projected distributions for 2030-A1B and 2030-A1FI show similar patterns that do not indicate drastic changes from the current predicted distribution. In the western region, a decrease in average habitat suitability in central locations has taken place, while new areas of low/average suitability appear east of extant habitat areas. In the east, a contraction of low/average habitat suitability has occurred in south central South Australia (Eyre
Peninsula). In the states of New South Wales (NSW) and Queensland (QLD), an expansion of low and average habitat suitability is predicted. Across the distribution, low suitability of habitat increased over that class in the current distribution substantially in both 2030-A1B (160,080 km²) and 2030-A1FI (177,960 km²) predicted distributions.

In 2070, projections made with our two climate scenarios are vastly different from each other, and the current predicted distribution (Figure 7.3). The projected distribution for 2070-A1B shows a vast increase in area for low (160,710 km²), average (127,790 km²), high (75,189 km²) and very high (15,051 km²) habitat suitability classes when compared with the current predicted distribution. High and very high habitat suitability classes are predominantly located in the eastern extent of Western Australia and the Murray-Darling Rivers Basin region of eastern South Australia and western New South Wales and Victoria. The projected distribution for 2070-A1FI also indicates an increased area of low, (171,025 km²), average (106,285 km²), high (65,270 km²) and very high (15,990 km²) habitat suitability classes when compared with the current predicted distribution. Whilst the projected distribution for the western region shows the same south-east trend toward increasing habitat suitability as 2070-A1B, projections for the eastern regions are very different. Habitat suitability for South Australia (particularly the east) has decreased substantially, with increasing suitability projected in Victoria, eastern New South Wales and Queensland outside the southern scrub-robin's current distribution.

*Spatial patterns of genetic dissimilarity and the environment*

The ALL GDM model for the entire sampling region was able to explain 57.2% of observed spatial genetic variation. Climatic variables (combined contribution: 0.611) far outweighed the contribution of substrate variables (combined contribution: 0.366) (Table 7.3). Of the climatic variables, water availability were the strongest contributors, the most important of which was the annual mean water deficit (WDEF_MEAN, 0.200) derived from a simple tipping bucket water balance model parameterised with soil attributes (SOLPAWHC). Other climatic variables with important contributions were the diurnal temperature range maximum (TRNGX, 0.110), maximum month
rainfall (RAINX, 0.100) and mean annual evaporation (EVAPM, 0.115) (Table 7.3). From among the substrate variables, soil bulk density (BDENSITY, 0.109) was the most important contributor. Geographic distance was not a significant contributor to observed genetic distances. This result matches expectations as expressed in the conceptual model of distribution and genetic-environmental relationships.

When considering the EAST and WEST regions separately, the associated smaller sample sizes resulted in higher levels of deviance in genetic dissimilarity explained among sample locations. The EAST region GDM model explained 75.3% of genetic dissimilarity variation among sample locations. Only two environmental predictors are shared with the ALL model; SOLDEPTH and VALLEYBOTTOM, representing substrate conditions. Substrate variables (combined contribution 0.362) were more important than climate variables (0.305) in the EAST model (Table 7.3). From among the substrate variables, soil profile depth (SOLDEPTH: 0.224) was the most important contributor. From among the climatic variables, annual temperature range (TRNGA) which is associated with distance from the coast, was the strongest contributor (0.176). Geographic distance also did not contribute to spatial patterns of genetic dissimilarity in the EAST region. In the WEST region GDM model, 97.2% of spatial genetic dissimilarity variation was explained by environmental predictors and geographic distance. Climatic variables (0.478) were the strongest contributors to the WEST model, followed by substrate variables (0.200) and geographic distance (0.132). Of the climatic variables, water availability (0.273) and temperature (0.205) contributed strongly (Table 7.3).

We chose not to consider the ALL model in any further analyses due to its explanatory power relative to that of the regional EAST and WEST models. A classification of the relationship between spatial patterns of genetic distance and environment for each of our two regional GDM models, applied to the relevant IBRA subregions, is a representation of predicted genetic dissimilarity (Figures 7.4 and 7.5).

In the EAST region model, colouring indicates that the northern Flinders Ranges, the tri-border area encompassing eastern South Australia and western Victoria and New South Wales, and coastal areas would all be both genetically dissimilar from each other, and other mapped areas (Figure 7.4). The Flinders Ranges however, appear to be only marginal habitat (Figure 7.5). In the WEST region model,
Figure 7.4 Classified generalised dissimilarity model predictions of genetic dissimilarity in the southern scrub-robin in Western Australia (WEST, bottom) and eastern Australia (EAST, top). Red dots indicate sampling locations and yellow dots indicate occurrence data for the southern scrub-robin from the Atlas of Australian Birds database (Birds Australia 2011). Similar map colours among regions (within each map) predict genetic similarity, while increasingly different colours predict increasing genetic dissimilarity.
Figure 7.5 Classified generalised dissimilarity model predictions of genetic dissimilarity in the southern scrub-robin, clipped using the current predicted MaxEnt distribution (Figure 2) and extant vegetation (NVIS v3.1) in Western Australia (WEST, bottom) and eastern Australia (EAST, top). Red dots indicate sampling locations. Similar map colours among regions (within each map) predict genetic similarity, while increasingly different colours predict increasing genetic dissimilarity.
genetic dissimilarity within the southern Wheatbelt is predicted to be low, but dissimilar to the northern Wheatbelt (KB and FP sample locations) and to a lesser extent, the eastern part of the study area.

Projections of the four climate change scenarios on the regional EAST and WEST models (Figures 7.6 and 7.7) reveal only small amounts of compositional change between current and future conditions, with all values lying below 0.2. This would represent up to a 20% difference in genetic composition at any location (0.01 degree grid cell) over a period of about 40 (1990-2030) to 80 (1990-2070) years. By 2030, the level of genetic change that we would expect given the modelled relationship in the EAST region is very low for both the 2030-A1B and 2030-A1FI scenarios, consistent with similarity in the emissions scenarios at this time (IPCC 2007b). In the GDM model for the WEST region, the level of predicted genetic change is slightly higher, particularly along the northern fringe of the region (Figure 7.6). These effects are slightly more pronounced in the 2030-A1FI scenario. This region however is outside that likely to be used by the scrub-robin given the predicted limits of suitable habitat (Figure 7.7). In 2070, predicted levels of genetic change are higher across both EAST and WEST regions.

In the EAST for the 2070 scenarios, the greatest level of change is predicted for the northern Flinders Ranges and coastal regions, and varies from 0.03-0.04 for the 2070-A1B scenario to 0.05-0.06 for the 2070-A1FI scenario (Figure 7.6). The Flinders Ranges however, are not predicted to remain climatically suitable for the species under the 2070-A1FI scenario (Figure 7.7). In the WEST, predicted changes are far more extreme. For the 2070-A1B scenario, changes in the habitable south west of Australia remain relatively small (0.03-0.04; Figure 7.6), but are exacerbated in the 2070-A1FI scenario. This is consistent with the considerable departures at this time in the climate modelling based on the emissions scenarios forcing the climate (IPCC2007). The genetically dissimilar region around FP is predicted to experience a similar pattern of compositional change, however the MaxEnt distribution predicts that the climate renders this region uninhabitable (Figure 7.7).
Figure 7.6 Generalised dissimilarity model output from regional EAST and WEST regional models showing the level of compositional (molecular) change expected under moderate (A1B) and high (A1F1) emissions scenarios depicted for 2030 (first row) and 2070 (second row). Amount of predicted change is indicated by the colour ramp ranging from low (dark green) through high compositional change (dark brown).
Figure 7.7 Generalised dissimilarity model output from regional EAST and WEST regional models showing the level of compositional (molecular) change expected under moderate (A1B) and high (A1F1) emissions scenarios depicted for 2030 (first row) and 2070 (second row). Amount of predicted change is indicated by the colour ramp ranging from low (dark green) through high compositional change (dark brown). Generalised dissimilarity model output was clipped using the appropriate future predicted MaxEnt distribution (Figure 7.3) and extant vegetation (NVIS v3.1).
Discussion

Many species are adapted to the environment in which they occur and, as a consequence, few are likely to be impervious to the current and forecast climatic changes. Conservation scientists have frequently focussed on the devastating potential effects of climate change on species distributions via species distribution modelling (SDM) frameworks (Parmesan and Yohe 2003), rather than developing adaptive in situ management options to cope with the forecast impacts. However, interest is growing in how to manage species for enhanced resilience and adaptation as the conditions to which they are adapted change (Byrne 2008a, b). The spatially explicit approach used in this paper enables the effect of both isolation-by-distance and environmental gradients on patterns of genetic variation to be considered simultaneously. By quantifying the relative effect of each on intraspecific genetic diversity it is possible to ascertain the role that the environment plays in shaping adaptive traits. Our comprehensive approach not only enables us to identify locations where genetic uniqueness offers the option to manage for in situ adaptation under climate change, but seeks to identify where genetic-environment relationships will realise the most pressure in the future. Furthermore by considering environmental adaptation alongside the projected effect of climate change on distributional patterns and land use configurations, we are better able to formulate judicious conservation recommendations.

Predicted effects of a changing climate on distribution

Under the climate scenarios considered within this study, a net increase in the amount and suitability of habitat for the southern scrub-robin is forecast. Losses of suitable habitat areas are unsurprisingly for the northern extent of the distribution around Francois Peron NP (FP) in Western Australia and the northern Flinders ranges encompassing Arkaroo Rock (AR). These areas represent the trailing edge of a range shift for the species. Increases in habitat are forecast to occur both on the fringes of and regions distant from the species’ current distribution. These areas represent the leading edge of potential range expansion for the species. Some areas, such as the projected eastward expansion of habitat suitability in Western Australia, could be an important opportunity for the persistence of the species. This region is on the fringe of areas already occupied by the southern scrub-robin and is not
under intensive agricultural production. This could facilitate an increase in abundance of the southern
scrub-robin among the western populations of the species. However, the climate scenarios we
employed cannot describe the finer spatial and temporal aspects of climate change. As a consequence,
they are unable to inform whether climatically suitable habitat will be available in both current and
future predicted areas consistently over time to allow for demographic expansion into newly suitable
regions (Early and Sax 2011). Climate change is unlikely to be a simple, gradual process, but rather a
highly dynamic one of fluctuations around an overarching trend of change (Easterling et al. 2000,
Wang and Schimel 2003, Early and Sax 2011). Such fluctuations can create gaps in the suitable
climate path, and in addition to other barriers, such as landscape features, can prevent migration into
new areas of suitable climatic space (Early and Sax 2011).

In eastern Australia, moderate climate change scenarios predict an increase in suitable habitat area in
the regions that are already the important mainstays of the species, and an extension eastward into
northern areas of the Murray-Darling Rivers Basin in central NSW. If climate change indeed follows
this scenario then the immediate future of the southern scrub-robin does not appear threatened by
climate per se. Effects on other aspects of habitat such as vegetation type, food sources and biotic
interactions are not considered here. They may still have important implications for the species’
persistence (Moller et al. 2004, Miller-Rushing et al. 2010). The high impact climate change scenario
(A1FI) for 2070 paints a much less optimistic picture, however. Large parts of the southern Murray-
Darling Rivers Basin (eastern South Australia), currently inhabited by the species, potentially will
experience a decline in habitat suitability. New areas of increased suitability are predicted for
agricultural regions having fragmented habitat across southern South Australia and Victoria, and
toward the east coast of Victoria and New South Wales. These are so distant from the current
distribution that they are unlikely to be occupied by the species without human assistance. Assisted
colonization, the process whereby individuals of a species are intentionally moved or translocated to a
new location from which they were previously absent, is one option sometimes advocated under such
circumstances (Kreyling et al. 2011). This approach is biologically risky, particularly due to imperfect
knowledge of the species’ ecology and the suitability of recipient ecosystems, and the potential for
adverse effects on the recipient ecosystem’s composition and function (Ricciardi and Simberloff 2009,
Kreyling et al. 2011, Vila and Hulme 2011). Where other conservation actions are still possible (e.g. habitat management, restoration and protection), as we believe they are for the southern scrub-robin, the risks and costs associated with assisted colonization make this action a low priority in the near term, but planning should not preclude options that may become necessary considerations under high levels of climate change.

Opportunities for adaptation

We were able to demonstrate a strong association between environmental gradients and genetic dissimilarity, particularly using our region-specific GDM models. Largely different sets of environmental gradients were associated with the spatial patterns of genetic dissimilarity in each region. Thomassen et. al. (2010) reported a similar result in their GDM assessment of environmentally-associated genetic distances for the wedge-billed woodcreeper (Glyphorynchus spirurus). These patterns suggest that the environmental processes shaping patterns of genetic variation are likely to be quite different between regions, and that modelling such relationships across the range of a widely distributed species could ignore key regional information. We did however; find some commonality among the EAST and the WEST region models, for which substrate characteristics and temperature were both important predictive groups for spatial patterns of genetic dissimilarity. Substrate characteristics themselves are unlikely to directly influence southern scrub-robins; however they are likely to be a proxy for differences in vegetation type, in combination with climate. Vegetation type strongly influences dispersal in the southern scrub-robin (Chapter 5), and plays a critical role in providing habitat structure and supports food resources at home sites (Chapter 6).

Distance was unable to explain any genetic variation across the eastern region GDM model, but did contribute to the western region model. Our results suggest that the genetic variation examined is able to explain substantial aspects of adaptive differentiation, particularly in the eastern region. While microsatellites are putatively a neutral marker (Schlotterer 2000, England et al. 2003), they may be subject to selective forces if linked to adaptive markers through a process referred to as hitch-hiking (Storz 2005b, Eggert et al. 2009, Montgomery et al. 2010, Meier et al. 2011). Alternatively, if
Our regional models suggest that temperature patterns are strongly associated with spatial patterns of genetic diversity, indicating that there may be regional differences in tolerance of temperature patterns and extremes. Temperature changes associated with climate change may have important implications for local persistence in the southern scrub-robin. Given that our distribution modelling suggests that the species is unlikely to persist at the northernmost extremes of its current distribution under even a moderate climate change scenario (i.e., low emission sensitivity, A1B), translocation of these birds to more southern locations is a potential conservation action. This will not only bolster general genetic diversity in recipient locations, but in so doing introduce new alleles that might, for example, confer better ability to survive higher temperatures. This may offer southern populations enhanced resilience to predicted climate change (Weeks et al. 2011). However it is also prudent to consider the potential drawbacks of such a plan. For instance, the risk of outbreeding depression should be carefully assessed (e.g. Frankham et al. 2011) prior to any translocations. These findings represent new considerations in conservation planning that may be at odds with current paradigms that focus on maintaining current levels of genetic variability and focus on the *in situ* preservation of genotypic examples. Such “static” paradigms may have limited relevance in the future, when conservation management will need to operate more “dynamically” in response to the likelihood of dramatic climate change impacts (Prober 2011).

We suggest that areas receiving heightened conservation action aimed at assisting the southern scrub-robin adapt to climate change should satisfy several criteria to ensure the greatest chance of success. Importantly, we should aim to protect genetically dissimilar populations and hence provide the species with the greatest opportunity for *in situ* adaptation. These regions should be predicted to remain climatically suitable under climate change and occur where large tracts of native vegetation remain. Furthermore, regions identified for heightened conservation action should be predicted to expect only
mild to moderate amounts of pressure from climate change on gene-environment relationships. Our GDM models contribute information about the current genetic-environment relationships and the predicted pressure those relationships are forecast to experience under a changing climate, but not the suitability of habitat to support the species. The combination of land use information (DEWR 2006) with the two modelling frameworks – the MaxEnt model describing the existence potential for the species based on current habitat relationships and the GDM models describing the genetic relationships with environment – provides a basis for inferring the capacity of habitat to support the species and the capacity of the species to adapt in situ to changes in surrounding habitat conditions. This evaluation suggests that regions that would benefit most from heightened enhanced conservation initiatives are those in central and south eastern Western Australia and in the south east and south west of South Australia. Populations in these regions would be ideal candidates for monitoring of abundance and genetic diversity. Additionally, heightened conservation action should focus on the increased control of feral predators and herbivores (Chapter 6) and the increased protection and expansion of appropriate habitat for territory establishment and reproduction (Chapter 6) and dispersal (Chapter 5). This would ensure a large effective population size and high levels of genetic diversity in the southern scrub-robin (Weeks et al. 2011). These conservation actions are also likely to assist the persistence of other ground dwelling bird species endemic to the mallee that are similarly threatened by introduced species and habitat loss, including the mallee fowl (Leipoa ocellata) and cinnamon quail thrush (Cinclosoma cinnamomeum). These areas identified for conservation action would also be ideal candidates for receiving translocated southern scrub-roins from northern regions.

Future empirical work

Our work was based on microsatellites, which are putatively neutral markers (Schlotterer 2000, England et al. 2003). Closer study is warranted of whether selection is operating, and it would be prudent to augment our findings by sampling a greater number of sites or ideally, the identification and use of adaptive markers.
Our investigation of environmental variables and their relationship to spatial patterns of genetic diversity is based on 17 locations from across a widespread species distribution. We extrapolated those relationships outside the immediate region of our sampling locations. To add weight to the findings of this study, we suggest that additional sampling be conducted. In particular this would be best placed to occur in Western Australia, where only five sites were located, and in areas which our GDM analyses predicted high genetic dissimilarity but were not sampled directly as part of this study.

**Conclusion**

In an era of habitat loss and climate change, species require comprehensive and sophisticated conservation strategies if they are to persist. Our approach brings together an understanding of species demography, characterises the nature of the anthropogenic threats, and elucidates the capacity of the species in question to respond. Distributional modelling suggests that climate change will increase the area of suitable habitat for the southern scrub-robin. However, this does not necessarily guarantee a secure future for the species because much of this potential future habitat currently supports agricultural activities and other areas have been earmarked for exploitation. Many of the future gains in suitable habitat are distant from the current distribution or occur in isolated agricultural fragments. As a species of low mobility, the territorial, ground-dwelling southern scrub-robin will not easily be able to migrate to distant suitable habitat. Facilitating resilience and adaptation to changing conditions (with the possibility of active translocation) will undoubtedly play important conservation roles for the species. We have identified areas in the landscape that through their relationship with the environment, are predicted to be genetically dissimilar to one another. Their ongoing protection should serve as the foundation for preserving genetic variability to facilitate adaptation to environmental change. Furthermore, from among these genetically disparate areas, we have identified those in both the western and eastern sectors of the southern scrub-robin’s current distribution that are forecast to remain climatically suitable, currently encompass large areas of native vegetation and whose molecular relationship with the climate is expected to experience minimal pressure. These regions are best placed to benefit from improved conservation actions and serve as centres of adaptive capacity over the coming century.
Acknowledgements

We acknowledge the assistance and support of Kathy Saint from the University of Adelaide and Alison Fitch from Flinders University. We also acknowledge Glenn Manion from the Office of Environment and Heritage, New South Wales State Government for permission to use and assistance with GDM software. This project was funded by CSIRO (Climate Adaptation Flagship), Department of Environment and Natural Resources in South Australia (Wildlife Conservation Fund), Sir Mark Mitchell Research Foundation, Birds Australia (Stuart Leslie Bird Research Award) and Australian Geographic Society.
Supplementary section

Table S7.1 Substrate GIS datasets used in modelling applications as environmental proxies to characterise relationships between the environment and demography for the southern scrub-robin.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Description</th>
<th>Derivation</th>
</tr>
</thead>
<tbody>
<tr>
<td>SOLDEPTH</td>
<td>Solum depth (surface and subsoil layers) (M)</td>
<td>The weighted average of the solum depth values provided by McKenzie et al. (2000). Note that for PPFs without a B horizon the solum depth was taken as equal to the A horizon depth. Units are m. Derived from Western and McKenzie (2004). Solum refers to the surface and subsoil layers that have undergone the same soil forming conditions.</td>
</tr>
<tr>
<td>SOLPAWHC</td>
<td>Plant-available soil water holding capacity (mm)</td>
<td>The weighted average of the solum plant available water holding capacity (PAWHC) values provided by McKenzie et al. (2000). Solum PAWHC is defined as the sum of the PAWHC for the A and B horizons, which are calculated as (field capacity – wilting point)*horizon depth. Note that for PPFs without a B horizon the solum PAWHC was taken as equal to the A horizon PAWHC. Units are mm. Derived from Western and McKenzie (2004).</td>
</tr>
<tr>
<td>KSAT</td>
<td>Solum average median horizon saturated hydraulic conductivity (Mm/h)</td>
<td>The weighted average of median solum horizon saturated hydraulic conductivity (ksat) provided by McKenzie et al. (2000). McKenzie et al. (2000) provided classes of median ksat on a logarithmic scale where each class has a range of half an order of magnitude. These classes were converted to actual values of ksat, which were then averaged. The final values were rounded back (in the logarithmic domain) to the same precision as the original classes but are provided in units of mm/h. Derived from Western and McKenzie (2004). Solum average of A and B horizons ksat values are weighted by the depth of each horizon.</td>
</tr>
<tr>
<td>CALCRETE</td>
<td>Calcrete in or below soil profile (presence)</td>
<td>The presence (1) or absence (0) of calcrete in or below the soil profile. Derived from McKenzie et al. (2000). Reported to be an under estimate for two reasons: some PPFs have a range of possible substrates including calcrete but it is misleading to record calcrete as present; many PPFs may overlie calcrete but this feature is not used as a criterion in classifying the soil type.</td>
</tr>
<tr>
<td>HPEDALITY</td>
<td>Hydrological scoring of pedality (score)</td>
<td>Hydrological scores for grades of pedality based on correlations with measured steady infiltration rates for a wide range of soils, as determined by Lin et al.(1999): single grain (50), massive (0), weak (1), moderate (5), or strong (25). In this classification, single grain is listed as a very strong class under ped grade to compare sand with other textural soils. Pedality derives from McKenzie et al. (2000).</td>
</tr>
<tr>
<td>COARSE</td>
<td>Soils dominated by coarse fragments including ironstone (class)</td>
<td>The Atlas of Australian soils annotates very gravelly soils through the use of prefixes. Soils (PPFs) with a KS- prefix have &gt; 60% ironstone coarse fragments throughout the profile (class 2); soils with a K- prefix have 60% or more coarse fragments other than ironstone (class 1); other soils that are not dominated by coarse fragments have no prefix (class 0).</td>
</tr>
<tr>
<td>CLAY</td>
<td>Solum average median clay content (%)</td>
<td>Estimated median percentage clay content of estimated soil texture. The estimated clay contents for 6 texture groups by McDonald et al. (1990) were used as a guide: interpreted values were increased or decreased depending on the type of soil within a group. Derived from McKenzie et al. (2000). The solum average clay content is the A and B horizon estimates weighted by the depth of each horizon.</td>
</tr>
<tr>
<td>Property</td>
<td>Description</td>
<td></td>
</tr>
<tr>
<td>-------------------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
<td></td>
</tr>
</tbody>
</table>
| BDENSITY          | **Solum average bulk density** *(Mg/m³)*  

Bulk density is a measure of a soil's mass per unit volume of soil and depends on the mineral composition of the soil and degree of compaction. Uncertainty in bulk density estimates will be greater than for texture as data are not available for many groups of soils. Bulk density is inversely related to soil porosity: the more pore space in a soil the lower the value for bulk density. Soils high in organics and some friable clay may have a lower bulk density. Derived from McKenzie *et al.* (2000). The solum average bulk density is the A and B horizon estimates weighted by the depth of each horizon. |
| NUTRIENTS         | **Gross nutrient status (Rating)**  

Gross nutrient status is a rating defined by McKenzie and Hook (1992) and included with the McKenzie *et al.* (2000) attributes. The interpretations relate to the behaviour of profiles under agricultural management. Profiles with a low nutrient status (class 1) exhibit major responses to N, P, and K fertilisation along with most micronutrients. Profiles with a moderate nutrient status (class 2) respond to N and P fertilisation with occasional responses to some micronutrients. It is uncommon for profiles with a high nutrient status (class 3) to respond to N and P fertilisation except after intensive farming. The main sources for the McKenzie and Hook (1992) assessment of nutrient status were Stace *et al.* (1968) and Northcote *et al.*. |
| FERT              | **Inherent rock fertility (Rating)**  

An index of inherent rock fertility by De Vries (2009) for the 1:1 million geology of Australia based on a scheme from the Broad Classification of Parent Material for Pedologic Purposes (Gray and Murphy 1999). The scheme ranks lithological types on a 1 to 6 scale from rocks that are extremely siliceous (>90% silica) with an extremely low base content (<3% Ca, Mg, Fe oxides) to those that are ultramafic (<45% silica and >30% base content). The original data range (1-6) has been multiplied by 2: values now range from very low fertility (2) to very high fertility (12). Rock voids without data including lakes were filled by neighbourhood statistics. |
| RELIABLE          | **Data levels support soil property interpretations (index)**  

An index of soil attribute reliability based on data sources available for interpretation. The interpretations of basic soil properties in McKenzie *et al.* (2000) are derived from the CSIRO National Soils Database where possible and the availability of this information is provided in index form where 1 = >20 profiles + ancillary information, 2 = 5-20 profiles + ancillary information and 3 = interpolated from other PPF interpretations. Values < 1 represent no-data areas (e.g. lakes and voids). The index reflects the relative data support for all subsequent interpretations. These indices were averaged using the weights in Table 1, 0.25 was then added to the average and the resulting value was rounded. This process provided a little more weight to the more uncertain PPFs in the soil landscape. Derived from Western and McKenzie (Western and McKenzie 2004). |
| GRAVITY           | **Bouguer gravity anomalies (Gal (acceleration))**  

The 2009 edition of the onshore gravity grid of Australia is a compilation of over 1.4 Million gravity stations using Bouguer gravity anomalies in *galileo* units of acceleration (Gal). The original resolution data were bilinear-resampled from 400m resolution to 1km. Small areas without data were filled by neighbourhood statistics. |
| MAGNETICS         | **Magnetic anomalies (nanoTesla (nT))**  

Magnetic anomaly grid of the Australian region, 3.1. (Petkovic and Milligan 2002). Magnetic anomaly unit is nanoTesla (nT). Appropriate IGRFs have been removed. Small areas without data were filled by neighbourhood statistics. |
| WII_WGS1KB        | **Weathering**  

A weathering intensity index (WII) with values ranging 0 to
The weathering intensity index was developed from regression models for erosional landscapes but has the potential to inform deposition processes and materials. As weathering intensity increases there are changes in the hydrological, geochemical and geophysical characteristics of the regolith.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Calculation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLOPE</td>
<td>Terrain slope (%)</td>
<td>Mean of the 9 second slope values in each 36 second grid cell (%), computed by Stein (2008).</td>
<td>Stein (2008)</td>
</tr>
<tr>
<td>RELIEF</td>
<td>Terrain relief (M)</td>
<td>Range of the 9 second DEM elevation values in each 36 second grid cell (m), computed by Stein (2008).</td>
<td>Stein (2008)</td>
</tr>
<tr>
<td>ROUGHNESS</td>
<td>Terrain roughness (%)</td>
<td>Coefficient of variation (Cv) of the 9 second DEM elevation values in each 36 second grid cell (m). Computed mean elevation values greater than -1 and less than +1 were set to a value of 1 to calculate the Cv (%), computed by Stein (2008).</td>
<td>Stein (2008)</td>
</tr>
<tr>
<td>TWI</td>
<td>Topographic wetness index (index)</td>
<td>Maximum of the Topographic Wetness Index (TWI) values in each 36 second grid cell. TWI was calculated as ( \ln(a/\tan \beta) ) where a is the upslope area per unit contour length and ( \tan \beta ) is the local slope (dimensionless), computed by Stein (2008).</td>
<td>Stein (2008)</td>
</tr>
<tr>
<td>MRVBF</td>
<td>Valley Bottom Flatness (index)</td>
<td>Median value of the multi-resolution Valley Bottom Flatness index values (mrVBF) in each 36 second grid cell (dimensionless), computed by Stein (2008), based on the method of Gallant and Dowling (2003).</td>
<td>Stein (2008)</td>
</tr>
<tr>
<td>MRRTF</td>
<td>Ridgetop Flatness (index)</td>
<td>Median value of the multi-resolution Ridgetop Flatness index values (mrRTF) in each 36 second grid cell (dimensionless), computed by Stein (2008).</td>
<td>Stein (2008)</td>
</tr>
<tr>
<td>VALLEYBOTTOM</td>
<td>Proportion Valley bottoms (%)</td>
<td>Proportion of the 9 second grid cells classed as valley bottoms according to the values of mrVBF and mrRTF (i.e. mrRF – mrRTF &gt;2) (%), computed by Stein (2008), based on the method of Gallant and Dowling (2003).</td>
<td>Stein (2008)</td>
</tr>
<tr>
<td>RIDGETOPFLAT</td>
<td>Proportion Ridge tops (%)</td>
<td>Proportion of the 9 second grid cells classed as ridgetop flats according to the values of mrVBF and mrRTF (i.e. mrRTF – mrVBF &gt;2) (%), computed by Stein (2008), based on the method of Gallant and Dowling (2003).</td>
<td>Stein (2008)</td>
</tr>
<tr>
<td>EROSIONAL</td>
<td>Proportion Erosional surfaces (%)</td>
<td>Proportion of the 9 second grid cells classed as valley bottoms according to the values of mrVBF and mrRTF (i.e. mrVBF &amp; mrRTF both &lt; 2.5) (%), computed by Stein (2008), based on the method of Gallant and Dowling (2003).</td>
<td>Stein (2008)</td>
</tr>
</tbody>
</table>
Table S7.2 Climate GIS datasets used in modelling applications as environmental proxies to characterise relationships between the environment and demography for the southern scrub-robin.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Description</th>
<th>Derivation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C4GI</strong></td>
<td>Growth index C4 megatherm plants (index)</td>
<td>Annual mean growth index for C4 megatherm plants, computed for a clay loam soil type with 150mm available water holding capacity, as the product of three component indices (temperature, light and moisture) using an optimum temperature of 32°C and range 10-45°C, derived from GROWEST module of ANUCLIM version 6.</td>
</tr>
<tr>
<td><strong>MEGAGI</strong></td>
<td>Growth index C3 macrotherm plants (index)</td>
<td>Annual mean growth index for C3 macrotherm plants, computed for a clay loam soil type with 150mm available water holding capacity, as the product of three component indices (temperature, light and moisture) using an optimum temperature of 28°C and range 10-38°C, derived from GROWEST module of ANUCLIM version 6.</td>
</tr>
<tr>
<td><strong>MESOGI</strong></td>
<td>Growth index C3 mesotherm plants (index)</td>
<td>Annual mean growth index for C3 mesotherm plants, computed for a clay loam soil type with 150mm available water holding capacity, as the product of three component indices (temperature, light and moisture) using an optimum temperature of 19°C and range 3-36°C, derived from GROWEST module of ANUCLIM version 6.</td>
</tr>
<tr>
<td><strong>MICROGI</strong></td>
<td>Growth index C3 microtherm plants (index)</td>
<td>Annual mean growth index for C3 microtherm plants, computed for a clay loam soil type with 150mm available water holding capacity, as the product of three component indices (temperature, light and moisture) using an optimum temperature of 10°C and range 0-20°C, derived from GROWEST module of ANUCLIM version 6.</td>
</tr>
<tr>
<td><strong>RHU215</strong></td>
<td>Relative Humidity 3pm (%)</td>
<td>Approximate monthly relative humidity defined as the amount of moisture in the air expressed as a percentage (ratio) of the amount of moisture present if the air was saturated at that temperature (3pm). Calculation follows Abbott and Tabony (1985).</td>
</tr>
<tr>
<td><strong>ARID</strong></td>
<td>Aridity index (Dimensionless)</td>
<td>The monthly ratio of precipitation to potential evaporation (pan, free-water surface). A numerical indicator of the degree of dryness of the climate at a given location. Adapted from the index proposed by UNEP (1992; cited in Middleton and Thomas (1997)).</td>
</tr>
<tr>
<td><strong>ADEF</strong></td>
<td>Precipitation deficit (mm)</td>
<td>The monthly difference between precipitation and potential evaporation (pan, free-water surface), without accounting for soil buffering capacity on water availability (after Harmsen et al. (2009), adapted from De Pauw (2002)). Also known as water deficit or hydrological deficit. Values are negative when evaporation demand is greater than rainfall indicating a water deficit.</td>
</tr>
<tr>
<td><strong>WPOT</strong></td>
<td>Soil water potential (MPa)</td>
<td>The monthly soil volumetric water content in units of pressure potential between field capacity (0 bars) and wilting point (-1.5 MPa), derived from a simple tipping-bucket model of water balance. Plant available soil water holding capacity for varying soil depths is defined by the attribute SOLPAWHC (Western and McKenzie 2004), derives from the Atlas of Australian Soils.</td>
</tr>
<tr>
<td><strong>WDEF</strong></td>
<td>Soil water deficit (mm)</td>
<td>The monthly residual evaporative demand that is in excess of soil moisture at wilting point (-15 Bars) including rainfall, derived from a simple tipping-bucket model of water balance. Very negative values represent a particularly marked soil water deficit. Plant available soil water holding capacity for varying soil depths is defined by the attribute SOLPAWHC (Western</td>
</tr>
<tr>
<td>Variable</td>
<td>Definition</td>
<td></td>
</tr>
<tr>
<td>----------</td>
<td>------------</td>
<td></td>
</tr>
<tr>
<td>EAE0</td>
<td><strong>Crop factor (Dimensionless)</strong></td>
<td>The monthly ratio of actual evapotranspiration to potential (pan, free-water surface) evaporation. Adapted from the index by Specht and Jones (1971). Actual evapotranspiration is an output of a simple tipping-bucket water balance model, and potential evaporation is an input (ie not adjusted by the coefficient of potential evapotranspiration, see PWAT). This ratio represents a water stress index and has been termed the ‘crop factor’ (Doorenbos and Pruitt 1975). Plant available soil water holding capacity for varying soil depths is defined by the attribute SOLPAWHC (Western and McKenzie 2004), derives from the Atlas of Australian Soils.</td>
</tr>
<tr>
<td>PWAT</td>
<td><strong>Water Stress Index (%)</strong></td>
<td>The monthly water stress is the ratio of actual to potential evapotranspiration expressed as a percentage. High water stress occurs when values are low or zero, low water stress occurs with higher values. Adapted from the index by Hackett (1988). Actual evapotranspiration is an output of a water balance model, and potential evapotranspiration is the pan evaporation (free-water surface) adjusted by the coefficient of potential evapotranspiration (PETCF). A constant PETCF value of 0.9 was used for all months which assumes constant leaf area index. Plant available soil water holding capacity for varying soil depths is defined by the attribute SOLPAWHC (Western and McKenzie 2004), derives from the Atlas of Australian Soils.</td>
</tr>
<tr>
<td>SPLS</td>
<td><strong>Soil water surplus (mm)</strong></td>
<td>The monthly precipitation that is in excess of maximum soil water holding capacity including evaporative demand, derived from a simple tipping-bucket model of water balance. Plant available soil water holding capacity for varying soil depths is defined by the attribute SOLPAWHC (Western and McKenzie 2004), derives from the Atlas of Australian Soils.</td>
</tr>
<tr>
<td>SRAIN1MP</td>
<td><strong>Solstice rainfall seasonality ratio (Dimensionless)</strong></td>
<td>Solstice rainfall seasonality is the ratio of summer to winter precipitation, where summer precipitation is defined as the sum of Dec-Jan-Feb precipitation and winter precipitation is defined as the sum of Jun-Jul-Aug precipitation</td>
</tr>
<tr>
<td>SRAIN2MP</td>
<td><strong>Equinox rainfall seasonality ratio (Dimensionless)</strong></td>
<td>Equinox rainfall seasonality is the ratio of spring to autumn precipitation, where spring precipitation is defined as the sum of Sep-Oct-Nov precipitation and autumn precipitation is defined as the sum of Mar-Apr-May precipitation</td>
</tr>
<tr>
<td>TRNG</td>
<td><strong>Diurnal temperature range (°C)</strong></td>
<td>Monthly climatic layers were computed with the ESOCCLIM module of ANUCLIM version 6.0 (beta) for each grid cell of a 0.01 degree resolution DEM derived by resampling the national 9 second DEM version 3 with the Arc/Info RESAMPLE function using bilinear interpolation.</td>
</tr>
<tr>
<td>SPLS</td>
<td><strong>Soil water surplus (mm)</strong></td>
<td></td>
</tr>
<tr>
<td>RAIN</td>
<td><strong>Rainfall (mm)</strong></td>
<td></td>
</tr>
<tr>
<td>RADN</td>
<td><strong>Rainfall-modified solar radiation (MJ/m²/day)</strong></td>
<td></td>
</tr>
<tr>
<td>MINT</td>
<td><strong>Minimum temperature (°C)</strong></td>
<td></td>
</tr>
<tr>
<td>MAXT</td>
<td><strong>Maximum temperature (°C)</strong></td>
<td></td>
</tr>
<tr>
<td>EVAP</td>
<td><strong>Evaporation (mm)</strong></td>
<td></td>
</tr>
</tbody>
</table>
Chapter 8:

General Discussion

Introduction

The aim of this thesis was to characterise the demography of the southern scrub-robin using molecular tools, across intact and fragmented mallee vegetation in southern Australia. I then employed this information to appraise species distribution modelling predictions under forecast climate change, and inform adaptive conservation planning.

The current use and potential role of molecular demography to inform species distribution modelling for conservation is reviewed as a precursor to my study of the southern scrub-robin (chapter 2). I then develop microsatellites for the southern scrub-robin in order to investigate contemporary demography (chapter 3). The effect of habitat fragmentation and protection (chapter 4), landscape type (chapter 5) and habitat quality (chapter 6) on demography is assessed using these microsatellites. I also explore the potential impacts of future climate change on the southern scrub-robins’ distribution and highlight opportunities to facilitate in situ adaptation (chapter 7). Within the present chapter, I discuss the key thesis findings, and identify future areas of research that will further assist conservation planning for the southern scrub-robin.

Understanding contemporary demography is key to accurate species distribution modelling

Predictions of anthropogenically-forced climate change have instigated the development of modelling tools seeking to elucidate what effect this might have on the future distribution of biodiversity (Pliscoff and Fuentes-Castillo 2011). A major limitation of many species distribution models is that they inherently assume species can track their climate envelope if it shifts, regardless of life history, demography or biotic interactions. Striving to more accurately predict the response of species distributions to climate change, modelling tools are now being refined to integrate species parameters,
including demography (Keith et al. 2008, Vos et al. 2008). In parallel, the development and application of molecular tools to understand historic and contemporary population demography has seen significant recent advances (Hendry et al. 2011, Sunnucks 2011). Despite the obvious potential for molecular tools to generate robust demographic parameters to inform modelling exercises, my literature review indicated that this was largely not the case (Chapter 2). In particular, uptake of contemporary demographic information to accurately model the future distribution of species has been extremely limited. Critically, I found none of the studies that used bioclimatic models to predict future distributions incorporated demographic information generated by molecular tools. Hence I feel that the identification of molecular approaches that characterise contemporary demography relevant to future species distribution modelling constitutes my most important contribution toward fostering more accurate predictions.

I highlight three important areas in which contemporary demography can contribute toward improved accuracy in bioclimatic modelling. The first of these is characterising gene flow. Understanding a species-specific ability to track its climate envelope through different landscape types is crucial to characterising the impact of climate change. Recently developed approaches including isolation by resistance (IBR) and linear mixed models (Yang 2004, Pavlacky et al. 2009, Chapter 5) are able to characterise gene flow via multiple potential pathways among populations. Linear mixed models in particular are able to distinguish between the contribution of historical and contemporary landscapes, as well as the effect of different landscape types to genetic connectivity (Pavlacky et al. 2009, Chapter 5). Likewise, identifying demographic and habitat features associated with both unstable and robust populations (Peery et al. 2006, Martinez-Solano and Gonzalez 2008, Peery et al. 2008, Chapters 4 and 6) is important to accurately model future species distributions. Healthy, self-sustaining populations are not only reliant on appropriate climate, but also the availability of suitable landscape features that facilitate large, well-connected populations. Finally, facilitating adaption to changing conditions will form a crucial part of contemporary conservation. By modelling the relationship between spatial patterns of molecular diversity and environmental gradients, it is possible prioritise areas most likely to facilitate adaption (Rouget et al. 2006, Bonin et al. 2007, Klein et al. 2009, Thomassen et al. 2010, Thomassen et al. 2011, Chapter 7). In the following section, I look in greater detail at how these
principles were applied to understand the molecular demography of the southern scrub-robin and inform its conservation under climate change.

The consequences of habitat loss and protection

Biodiversity worldwide is at threat from the ongoing activities of human populations, particularly urbanisation and agriculture. The inevitable loss of habitat stemming from these activities frequently leads to increased levels of between population diversity and reduced levels of within population diversity (Templeton et al. 1990, Keyghobadi 2007). Contrary to expectation, these patterns were not evident for the southern scrub-robin (Chapter 4). In fact, within population genetic diversity was highest in agricultural matrices. Furthermore, low between population diversity, population clustering and levels of recent migration all suggest agricultural clearing has had a minimal impact on the microevolutionary processes of the southern scrub-robin. A closer look at the amount and spatial configuration of remnant vegetation suggests that most sampling locations in the agricultural matrices were not highly isolated from larger tracts of vegetation. Proximity to other areas of native vegetation may be enabling gene flow among populations of the southern scrub-robin, maintaining high effective population sizes and minimising inbreeding and genetic drift. Populations only moderately isolated frequently experience comparatively smaller effects on within and between population genetic diversity than those highly isolated by habitat fragmentation (Mech and Hallett 2001, Segelbacher et al. 2003, Andersen et al. 2004, Johansson et al. 2005). Supporting this idea I found the predicted effects of habitat loss and fragmentation are evident in the smallest, most isolated populations in the agricultural matrices; i.e. diminished within population genetic diversity, increased levels of between population diversity, and increased levels of inbreeding.

In both Western and South Australia, within population genetic diversity was positively correlated with latitude, producing a pattern consistent with the abundant centre hypothesis (Chapter 4). The abundant centre hypothesis proposes that local environmental conditions should be superior at the centre, relative to the range extremities of a species distribution. From a molecular perspective, my results reflect the expectation of reduced genetic diversity and increased genetic structure in
populations progressively closer to range margins (Vucetich and Waite 2003, Eckert et al. 2008). This pattern is at odds with protected areas network across the mallee region of southern Australia, wherein conservation parks are predominately found at lower latitudes in regions where soils and climate and less favourable to agriculture, a pattern systemic across Australia (Fuller et al. 2010). Hence the regions that were best placed to sustain large, genetically diverse populations of the southern scrub-robin able to assist the species surmount future environmental challenges have suffered substantial amounts of habitat loss.

From a conservation perspective, this places the southern scrub-robin between a rock and a hard place. It would appear the Flinders Ranges are unlikely to offer a contemporary genetic refugium in South Australia, given its low levels of genetic diversity, and high levels of genetic differentiation from other locations. Additionally, the potential effects of climate change on these and other lower latitude populations suggest that large conservation areas may no longer be climatically suitable in the twenty-first century (Chapter 7). The scrub-robin may well be forced to subsist predominately in agricultural matrices. To further understand the demography of this species, and its ability to tackle contemporary environmental challenges, I also investigated the effects of landscape characteristics on gene flow and genetic diversity at home sites.

**Landscape type influences dispersal**

Dispersal is a critical aspect of species demography. Through dispersal, microevolutionary processes such as gene flow and drift occur, driving aspects of demography including effective population size, and spatial patterns of genetic diversity (Lowe et al. 2004, Hendry et al. 2011). Dispersal, and hence microevolutionary processes, may be mediated by different landscape types. Through their different resources and risks, landscape types may either facilitate or impede successful dispersal (Ricketts 2001, Pavlacky et al. 2009). The ecological modelling undertaken in this study, highlighted the fundamental nature of understorey structure to the southern scrub-robin, typically an important component of dispersal habitat for ground-dwelling birds (Sieving et al. 1996, Reid et al. 2004, Vergara and Simonetti 2006, Tomasevic and Estades 2008, Pavlacky et al. 2009). Hypotheses drawn
from this model predicted that landscape types lacking substantive understorey would expose dispersing southern scrub-robins to extreme weather and increased predation risk, while providing fewer foraging opportunities. These predictions were supported by results from historic and contemporary landscape contributions to observed spatial patterns of between population genetic diversity (Chapter 5).

Both chenopod and hummock grassland understorey types strongly inhibited dispersal in the historic and contemporary landscapes, with a model averaged effect stronger than geographic distance. Despite having very different structural characteristics, both these landscape types have an understorey that exposes the dispersing southern scrub-robin to inclement weather and ground hunting predators. Hummock grassland habitat normally has a eucalypt overstory, while the dominant spinifex understorey is composed of spikey stiff blades impenetrable to the southern scrub-robin. Conversely, chenopod habitat frequently lacks an overstory, and is dominated by saltbush and/or bluebush species in a low, open structure. The depauperate structure of the chenopod habitat also probably provides fewer foraging opportunities, particularly from among the ant fauna (Andersen 1983, Dangerfield et al. 2003) that constitute a large part of this species diet (Higgins and Peter 2002).

Landscape types more conducive to the southern scrub-robin’s requirements, primarily characterised by an accessible understorey, facilitated dispersal. These results however, were less conclusive. Landscape types with a shrubby understorey, which constitute important territory habitat for the species (Chapter 6), may in some instances inhibit dispersal. Aggressive interactions from southern scrub-robins with established territories may prevent dispersing conspecifics passing through (Hestbeck 1982, Matthysen 2005, Pavlacky et al. 2009). Alternatively, if suitable shrubby habitat is located and a territory successfully established, then continued dispersal is unwarranted and unlikely.

In the contemporary landscape, novel threats to dispersal emerge, particularly habitat loss due to agriculture, and introduced predators. Habitat loss, whilst impeding gene flow as hypothesised, did not have a particularly strong impact on patterns of between population genetic diversity. As discussed previously, high vegetation remnancy and low levels of fragmentation may have helped mitigate the
effects of habitat loss on demographic and microevolutionary processes. Habitat loss is also known to act in synergy with other human-based threats, such as introduced predators. The introduced fox frequently has its most profound effect on biodiversity in vegetated areas adjacent to agricultural reserves (Pita et al. 2009, Arthur et al. 2010). This phenomenon may explain the increased influence of chenopod toward decreasing dispersal in the contemporary landscape.

The effect of introduced predators and habitat loss is unlikely to be limited to dispersal. I characterised these and other aspects of habitat quality at scrub-robin territories, to gauge their impact on within population genetic diversity.

**Habitat quality and the role of introduced species**

Dispersal is only one aspect of species demography driving microevolutionary processes and spatial patterns of between population genetic diversity. In order for gene flow to occur, dispersing individuals must not only survive their journey, but locate habitat to support themselves, potential mates, and their juvenile offspring (i.e. establish). Habitat quality is thus a strong driver of both individual fitness and metapopulation dynamics (Pulliam 1988, 2000, Mortelliti et al. 2010).

Key amongst my findings were that introduced species were consistently associated with reduced habitat quality (as indicated by genetic diversity metrics) for the southern scrub-robin (Chapter 6). Increasing fox densities were associated with decreasing genetic diversity (as were cats) and effective population size, and increasing population structure. Foxes are known to be particularly successful in predating ground-dwelling species (Edwards et al. 2004), and are an identified predator of nestlings in the southern scrub-robin (Luck et al. 1999). It comes then as no surprise that these feral species were associated with several measures of reduced habitat quality. Predation by both the feral cat and the European red fox are listed as key threatening processes on the Environment Protection and Biodiversity Conservation Act (Department of Sustainability 2011). Ongoing eradication measure for these two species has failed to control their numbers and expansion across Australia (Edwards et al. 2004). However frequent baiting and other control measures for feral predators are practiced by many
of the conservation properties that participated in this study and these same properties concomitantly reported the lowest reported sightings for cats and foxes. A more co-ordinated and sustained feral predator control strategy across the Murray Mallee agricultural region would undoubtedly also benefit the southern scrub-robin and many other indigenous species.

As with patterns of dispersal (Chapter 5), vegetation characteristics also played an important role in determining habitat quality for the southern scrub-robin (Chapter 6). The presence of weeds was associated with decreased habitat quality. Weeds are known to alter available foraging opportunities as well as ecosystem processes when they invade an ecosystem, often making them less suitable for indigenous resident species (Levine et al. 2003). Shrubby understory was strongly negatively correlated with inbreeding, confirming this structural characteristic as a fundamental habitat component for the southern scrub-robin. Furthermore, tree cover (and leaf litter) was associated with decreased habitat quality. While recognising the importance of trees to the southern scrub-robin as a high point for territorial vocalisations and observations, I suggest that increasing tree dominance in a landscape may critically reduce the prevalence of shrubs.

The importance of shrubby habitat to both habitat quality (Chapter 6) and dispersal (Chapter 5), suggests that the prevalence of feral herbivores may be just as critical to southern scrub-robin persistence as feral predators. Feral herbivores, particularly rabbits (Oryctolagus cuniculus) and goats (Capra hircus) are common throughout the mallee habitat preferred by the southern scrub-robin. Feral herbivores change the structure and/or species composition of native vegetation in an ecosystem via both their foraging and movement (Edwards et al. 2004). Critically, the effects of feral herbivores are generally most pronounced at the ground level. Further investigation into the role of feral herbivores in altering habitat composition and quality for the southern scrub-robin is clearly warranted.

**Adapting to a future of change and stress**

Characterising the microevolutionary processes that sustain high effective population size and genetic diversity are critical to conservation management of the southern scrub-robin. In the case of climate
change, ascertaining which environmental variables drive patterns of intraspecific spatial genetic diversity can help identify areas that are genetically distinct in the landscape (Thomassen et al. 2010, Thomassen et al. 2011). These unique regions may be best placed to help facilitate adaptation to climate change.

Climate change is predicted to have strong impacts on the distribution of the southern scrub-robin, particularly by 2070 (Chapter 7). Under the moderate climate change scenario for 2070, substantial increases in both habitat suitability and total amount of habitat are forecast. While this is an encouraging result, it certainly doesn’t guarantee a secure future for the species. Although climate change may not directly threaten the southern scrub-robin, indirectly there may be impacts on food availability, biotic interactions, and other critical aspects of habitat such as vegetation composition and structure (Chapter 6) (Moller et al. 2004, Miller-Rushing et al. 2010). Furthermore, climate change is unlikely to be a unidirectional process, but rather characterised by dynamic fluctuations around a gradual trend of change (Easterling et al. 2000, Wang and Schimel 2003, Early and Sax 2011). This may create gaps in the climate path and together with landscape barriers inhibit migration into newly available areas of suitable climatic space (Early and Sax 2011). The uptake of new areas of suitable climatic space is also likely to be mediated by the presence of other important aspects of habitat, such as the availability of critical shrubby understorey for both dispersal (Chapter 5) and territory establishment (Chapter 6).

The high impact scenario for 2070 paints a far less optimistic picture. While gains in habitat in southern Western Australia and along the east coast of Australia are predicted, substantial losses of current habitat across large conservation areas are forecast in the southern Murray-Darling Rivers Basin. Furthermore, as many of the habitat gains are distant to the current distribution they are unlikely to be naturally colonized by the southern scrub-robin. This scenario in particular suggests that facilitating in situ adaptation to changing conditions will be an important conservation initiative for the southern scrub-robin.
My analyses demonstrate a strong relationship between spatial patterns of genetic diversity and environmental gradients in both eastern and western Australia and identify several areas of genetic dissimilarity. In the west, central and south easterly regions are most likely to provide evolutionary potential under climate change. In the east, the south east and south west of South Australia provide a similar opportunity. In highlighting these regions I considered several criteria that would heighten the chances of successfully providing evolutionary potential to the species. Firstly, the regions are genetically dissimilar to one another. These areas also exist within the current distribution of the species, are predicted to remain climatically suitable in both 2030 and 2070, and occur where large tracts of native vegetation remain. Furthermore, the molecular-environment relationships in these regions are predicted to experience minimal pressure under climate change. These criteria give preference to genetically unique populations not only able to persist into the future, but also best placed to maintain the microevolutionary processes that generate genetic diversity. I suggest that to protect and enhance evolutionary potential, these regions should receive improved conservation initiatives. Conservation actions should initially focus on feral animal control to improve dispersal success (Chapter 5) and habitat quality (Chapter 6). Over time, increasing habitat quality and amount, particularly for territory establishment, should focus on providing complex understory structure (Chapter 6). The regions I have highlighted may also benefit from receiving translocated individuals from lower latitude areas that are predicted to quickly become climatically unsuitable (Weeks et al. 2011). These individuals may confer increased tolerance of high temperatures and thus greater resilience to climate change.

Conclusion

The southern scrub-robin is a species for which many of its life-history traits predispose it to risk from anthropogenic changes to the environment. A substantial proportion of its current distribution is under agricultural production, yet little empirical work prior to this study had been completed to understand its effects on the scrub-robin. I characterised several demographic parameters for the southern scrub-robin across conservation and agricultural regions in both eastern and western Australia. Furthermore, I sought to understand both the risks and opportunities that climate change brings to the species by
modelling the relationship between the climate and both distribution and genetic diversity. By elucidating which aspects of the environment shape microevolutionary processes in the southern scrub-robin, I have provided an improved basis for informing judicious conservation initiatives that will help ensure the future of this species beyond the twenty-first century.
Appendix

Appendix A.1: References screened for data used in Chapter 2, Figure 2.1 and their classification

DNA Informed

Ancient Past


Inferred Future


Past and Inferred Future


No DNA Information Utilised

Ancient Past


Recent Past


**Inferred Future**


**Modelled Future**


Byrne, M. 2008a. Evidence for multiple refugia at different time scales during Pleistocene climatic oscillations in southern Australia inferred from phylogeography. Quaternary Science Reviews 27:2576-2585.


http://taylor0.biology.ucla.edu/structureHarvester/.


Holper, P. 2007. Climate change in Australia. CSIRO and Bureau of Meteorology.


Hughes, L. 2011. Climate change and Australia: key vulnerable regions. Regional Environmental Change 11:S189-S195.


McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. Available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html.


Priddel, D., R. Wheeler, and P. Copley. 2007. Does the integrity or structure of mallee habitat influence the degree of Fox predation on Malleefowl (Leipoa ocellata)? Emu 107:100-107.


Williams, K. J. 2010a. 1km resolution climatic layers fo continental analysis of biodiversity pattern (metadata fo digital spatial data). CSIRO Ecosystem Sciences, Canberra.
Williams, K. J. 2010b. 1km resolution terrain and substrate layers for continental analysis of biodiversity pattern (metadata for digital spatial data). CSIRO Ecosystem Sciences, Canberra.


